台灣農業研究

JOURNAL OF TAIWAN AGRICULTURAL RESEARCH

Vol.74 No.2 2025

Feature Articles

89 Farmers' Incentives and the Adoption of Sustainable Plant Protection Approaches
Po-An Lin, Wan-Yi Liao, Shuay-Tsyr Ho, Chia-Wei Hsieh, and Tsung-Han Li

113 Advancing Invasive Ant Management: Innovative and Targeted Strategies
Fang-Ling Chloe Liu, Shu-Ping Tseng, Chung-Chi Lin, and Chin-Cheng Scotty Yang

129 Effects of Carbon Dioxide Enrichment on Photosynthesis, Growth, and Flowering of *Phalaenopsis*
Ming-Hsuan Tsai and Wei-Ling Chen

141 Exploring the Biological Functions of Plant Volatile Organic Compounds
Chia-Hsun Ho, Man-Hsia Yang, Chiao-Ling Hsiao, and Ya-Ling Hou

Research Articles

151 Evaluation of Reflectometry and Refractometry for Rapid Sugar Detection in Sweet Potatoes
Hui-Ying Hou, Che-Lun Huang, I-Chi Yeh, and Yung-Chang Lai

161 Effect of Temperature on the Mycelium Growth and Sporulation of Four Pathotypes of *Pyricularia oryzae* in Taiwan
Yi-Nian Chen, Dong-Hong Wu, Mei-Chun Chen, and Pei-Chen Chen

177 Evaluation of the Use of One-Step Quantitative RT-PCR for Detection of Potato Virus X
Cheng-Ping Kuan, Ya-Ting Liu, Ssu-Yu Lin, Mei-Ju Lin, Shu Chen, and Yin-Hewey Cheng

189 A Revised Checklist of Insects and Mites of Rice from Taiwan
Shou-Horng Huang, Po-Yu Lai, and Tai-Chuan Wang

ISSN 2790-086X

Published by Taiwan Agricultural Research Institute, Ministry of Agriculture

台灣農業研究 JOURNAL OF TAIWAN AGRICULTURAL RESEARCH Vol.74 No.2 2025

ISSN 2790-086X
DOI:10.6156/JTAR

台灣農業研究

JOURNAL OF TAIWAN AGRICULTURAL RESEARCH

Vol.74 No.2 2025

專題論述

83 農民採用永續植物保護措施的誘因
林柏安、廖婉頤、何率慈、謝佳維、李宗翰

113 入侵螞蟻防治新趨勢：創新技術與精準整合策略
劉芳綾、曾書萍、林宗岐、楊景程

129 二氧化碳補充對蝴蝶蘭光合作用及生長開花之影響
蔡明軒、陳葦玲

141 探討植物揮發性有機化合物的生物性功能
何佳勳、楊滿霞、蕭巧玲、侯雅玲

研究報告

151 應用反射光度法及折射光度法於甘藷糖類含量快速檢測之可行性評估
侯惠盈、黃哲倫、葉亦琪、賴永昌

161 溫度對臺灣稻熱病菌 (*Pyricularia oryzae*) 四種病原型菌株生長及產孢之影響
陳繹年、吳東鴻、陳美君、陳珮臻

177 使用單步驟定量RT-PCR法於馬鈴薯X病毒檢測之評估
關政平、劉雅婷、林思妤、林玫珠、陳述、鄭櫻慧

189 臺灣水稻害蟲名錄之修訂
黃守宏、賴柏羽、王泰權

農業部農業試驗所出版

《台灣農業研究》編審會

總編輯

石憲宗／農業試驗所應用動物組

副總編輯

吳東鴻／農業試驗所作物組
許健輝／農業試驗所農業化學組

領域主編 (按筆劃序)

王強生／國立中興大學農藝學系
古新梅／國立中興大學農藝學系
安寶貞／農業試驗所植物病理組
呂秀英／苗栗區農業改良場
杜宜殷／國立臺灣大學園藝暨景觀學系
林彥蓉／國立臺灣大學農藝學系
林慧玲／國立中興大學園藝學系
侯豐男／國立中興大學昆蟲學系
陳右人／國立臺灣大學園藝暨景觀學系
陳世銘／國立臺灣大學生物產業機電工程學系
陳健忠／農業試驗所應用動物組
陳琦玲／農業試驗所農業化學組
張永和／私立靜宜大學食品營養系
張瑞璋／農業藥物試驗所
莊愷瑋／國立中興大學農藝學系
郭寶錚／國立中興大學農藝學系
黃炳文／國立中興大學應用經濟學系
黃振文／國立中興大學植物病理學系
黃裕銘／國立中興大學土壤環境科學系
黃肇家／農業試驗所作物組
楊正澤／國立中興大學昆蟲學系
楊純明／農業試驗所作物組
路光暉／國立中興大學昆蟲學系
鄒裕民／國立中興大學土壤環境科學系
劉力瑜／國立臺灣大學農藝學系
蔡致榮／農業試驗所
鍾文鑫／國立中興大學植物病理學系
顏國欽／國立中興大學食品暨應用生物科技學系

英文主編 (按筆劃序)

王寅東／美國德州農工大學
張宗仁／美國喬治亞大學
楊景程／美國佛吉尼亞理工大學
鍾光仁／國立中興大學植物病理學系

編輯助理

王立蓉／《台灣農業研究》期刊編輯室

台灣農業研究

第七十四卷　第二期　　中華民國一一四年六月三十日

出版者　農業部農業試驗所
發行人　林學詩
總編輯　石憲宗
地址　413008 臺中市霧峰區萬豐里中正路 189 號
網址　https://www.tari.gov.tw/jtar
電話　(04)2331-7236
E-mail　jtar@tari.gov.tw
線上投審稿系統　https://www.ipress.tw/J0042
台灣農業研究之稿約格式內容，詳自農業部農業試驗所首頁下列路徑下載：文宣出版 > 台灣農業研究 > 出版品稿約

編印　華藝學術出版部
地址　234634 新北市永和區成功路一段 80 號 18 樓
電話　(02)2926-6006
E-mail　press@airiti.com

定價　新臺幣一七五元
展售門市
1. 國家書店 / 104472 臺北市松江路 209 號 1 樓 / 電話 : (02)2518-0207
   國家網路書店 http://www.govbooks.com.tw
2. 五南文化廣場 / 400002 臺中市中山路 6 號 / 電話 : (04)2226-0330

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):87–112 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0001

Feature Article

Farmers' Incentives and the Adoption of Sustainable Plant Protection Approaches

Po-An Lin[1,*], Wan-Yi Liao[2], Shuay-Tsyr Ho[3], Chia-Wei Hsieh[4], and Tsung-Han Li[5]

Abstract

Lin, P. A., W. Y. Liao, S. T. Ho, C. W. Hsieh, and T. H. Li. 2025. Farmers' incentives and the adoption of sustainable plant protection approaches. J. Taiwan Agric. Res. 74(2):87–112.

Adopting sustainable plant protection approaches (SPPAs) is critical for addressing environmental challenges and ensuring sustainable agricultural systems. This review synthesizes current knowledge on the factors influencing farmers' adoption of SPPAs, focusing on behavioral, social, and institutional drivers. Farm-related determinants include health concerns, risk perceptions, economic stability, and literacy regarding SPPA benefits and implementation. Non-farm factors such as social norms, government policies, and stakeholder interactions also shape adoption behaviors. The role of social networks and extension services is underscored as critical mechanisms for knowledge transfer and motivation, with farmer-to-farmer interactions emerging as particularly influential. Despite evidence supporting the environmental and economic benefits of SPPAs, barriers such as high costs, perceived inefficacy, and limited access to information and technical resources persist. Government interventions, including subsidies, training programs, and crop insurance, are identified as key tools to mitigate risks and financial burdens associated with SPPAs. However, systemic issues, such as fragmented policies and conflicting market pressures, often hinder the adoption of SPPAs. This review highlights the need for integrated, evidence-based strategies that align incentives across stakeholders, leverage psychological insights into behavior change, and address regional and cultural differences in agricultural systems. Advancing SPPA adoption requires long-term research and coordinated efforts among researchers, policymakers, and the agricultural community to build resilient and sustainable farming practices globally.

Key words: Farmers' behavior, Integrated pest management (IPM), Agricultural sustainability, Agricultural policy, Stakeholders.

INTRODUCTION

As the human population continues to rise, our environment is facing unprecedented threats (IPCC 2021). Particularly, in an agricultural context, the demand for food is rising (Tilman *et al.* 2011). However, climate change has increased the frequency and severity of many abiotic stresses which have increased the challenges in maintaining food production in many regions (IPCC 2021). Influenced by the fluctuation in abiotic conditions, biotic challenges increase, including emerging and spreading pests and pathogens that lead to severe yield loss worldwide (Savary *et al.* 2019; IPPC 2021; Schneider *et al.* 2022). To combat these biotic challenges, synthetic pesti-

Received: February 20, 2025; Accepted: April 2, 2025.
[*] Corresponding author, e-mail: poanlin@ntu.edu.tw
[1] Assistant Professor, Department of Entomology, National Taiwan University, Taipei, Taiwan, ROC.
[2] Researcher and Product Manager, R&D Department, Good Farms, Tainan City, Taiwan, ROC.
[3] Assistant Professor, Department of Agricultural Economics, National Taiwan University, Taipei, Taiwan, ROC.
[4] Undergraduate Student, Department of Entomology, National Taiwan University, Taipei, Taiwan, ROC.
[5] Assistant Research Fellow, Pesticide Application Division, Agricultural Chemicals Research Institute, Taichung City, Taiwan, ROC.

cides have been used as one of the key methods that effectively inhibit the spread and growth of pests and pathogens since the Green Revolution have now become the single most commonly used approach of plant protection against biotic stresses (Matthews 2018). However, it is also well established that the unsustainable and excessive use of pesticides can be damaging to the environment and human societies (Lundgren & Fausti 2015; Sánchez-Bayo 2021), and it is now widely recognized in academia, most governments, and societies that transitioning away from the heavy reliance of unsustainable use of synthetic pesticide is a key way to a sustainable food production system (Horrigan *et al.* 2002; Wezel *et al.* 2014; Barzman *et al.* 2015; Finger *et al.* 2024).

Sustainable plant protection approaches (SPPAs) are defined as plant protection tools or behaviors that aim to control pests and pathogens in a way that is both environmentally sustainable and economically viable over the long term, prioritizing income stability and resilience rather than short-term profit maximization (Finger *et al.* 2024). This definition does not exclude the use of synthetic pesticides as a plant protection approach. When the application of pesticide is scientifically evaluated to be more environmentally friendly and sustainable, it can also be considered as a behavioral SPPAs (Lykogianni *et al.* 2021; Finger *et al.* 2024). Other tools of plant protection are believed to be innately more sustainable including, the use of biological control agents (Baker *et al.* 2020; Tomar *et al.* 2024), natural products (Thuerig & Tamm 2020), ecological farming practices (e.g., intercropping, crop rotation, trap crop, cover crop, agroforestry) (Deguine *et al.* 2023). While these sustainable approaches have been proven in some cases to lead to good pest control outcomes (Deguine *et al.* 2023), they are far from frequently adopted by farmers around the world (Finger *et al.* 2024).

Agriculture has changed throughout history, and in modern years, the main scheme of agriculture has been heavily influenced by the Green Revolution, which leads to agricultural industrialization. Agricultural industrialization is the process of using advanced technology, machinery, and scientific techniques to increase agricultural productivity and efficiency (Evenson & Gollin 2003). This involves the adoption of high-yield crop varieties, synthetic fertilizers, pesticides, and irrigation systems, as well as the integration of farming with large-scale production, processing, and distribution systems. This shift has transformed agriculture into a more mechanized and intensive industry, focused on maximizing output and improving cost-efficiency to meet the increasing demands of global food markets (Evenson & Gollin 2003). Although the industrialization of agriculture and productivism perspective has improved productivity across many regions globally, the prioritization of profit and productivity, along with the neglect of other agricultural values (such as ecosystem services), has led to numerous unsustainable issues in recent years (Deguine *et al.* 2021). This has also led to rigidity in production practices, particularly in pest control methods, where reliance on established practices makes farmers less likely to adopt alternative approaches, creating significant barriers to transforming agricultural production systems (Béné *et al.* 2019; Finger *et al.* 2024).

From the perspective of pest control, synthetic pesticides provide an effective and predictable means of eliminating pests in the short term, a level of efficacy unmatched by more sustainable approaches (Deguine *et al.* 2021). These sustainable methods, while less effective in the short term, protect crops over time, sustain soil and land fertility, and offer additional benefits such as maintaining ecosystem functions and addressing the environmental challenges posed by synthetic pesticides (Deguine *et al.* 2023). To enhance the adoption of SPPAs and promote a sustainable agricultural system, there is a constant effort to develop SPPAs that are as effective as synthetic pesticides and meet the productivity standards of modern agricultural production systems (Finger *et al.* 2024). However, despite the availability of effective SPPAs, farmers do not always adopt these mea-

sures. Recognizing this issue, it is important to understand the willingness and incentives of farmers in choosing plant protection practices. Identifying factors that change farmer behavior into adopting SPPAs could be key to establishing a more sustainable plant protection scheme.

With that said, there is a significant lack of comprehensive reviews on this specific topic (see Finger *et al.* 2024). To address this knowledge gap, this review aims to bridge the divide between identifying the causes of low adoption rates and proposing solutions to increase the use of SPPAs. The review will be divided into three sections: first, summarizing and synthesizing key farm-related and non-farm factors influencing farmers' incentives to adopt SPPAs on a global scale; second, examining the role of various stakeholders in shaping adoption decisions; and finally, discussing the key challenges and potential solutions for enhancing the adoption of SPPAs.

FACTORS DETERMINING THE SPPAS ADOPTION BY FARMERS

The adoption of SPPAs is a behavioral process influenced by a complex interplay of factors (Fig. 1), similar to other human behaviors, making it challenging to disentangle these determinants

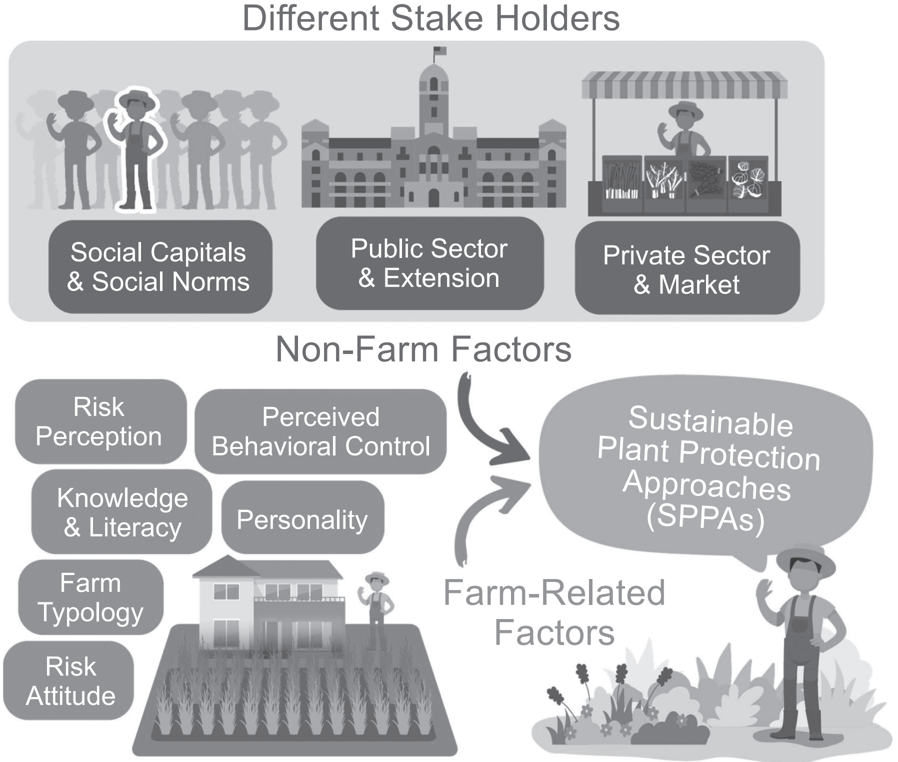

Fig. 1. Drivers of farmers' behavior and the adoption of sustainable plant protection approaches (SPPAs). This conceptual framework illustrates the interplay between farm-related and non-farm factors influencing farmers' adoption of SPPA practices. Farm-related factors include farm type, risk attitude, risk perception, knowledge, and literacy, which shape farmers' ability and willingness to implement SPPAs. Non-farm factors, such as social capital and norms, public sector policies and extension services, and market-driven incentives from the private sector, further interact to drive behavioral changes. Personality traits and perceived behavioral control act as cross-cutting influences between these domains. The figure highlights how these interconnected drivers collectively affect the adoption of SPPAs, emphasizing the complexity and multidimensional nature of farmers' decision-making processes.

(Albarracín *et al.* 2024). Recent studies, however, have identified key factors shaping farmers' decisions and behaviors regarding the use of SPPAs. These factors can broadly be categorized into two groups: farm-related factors and non-farm factors. Farm-related factors include personality (Knapp *et al.* 2021), relationships with nature (Yoshida *et al.* 2018), trust in information sources (Jin *et al.* 2015), risk tolerance (Begho 2021), risk perception (Toma & Mathijs 2007), knowledge (Shahidullah *et al.* 2023), beliefs (Ataei *et al.* 2021), perceived behavioral control (Dessart *et al.* 2019), and farm characteristics (Meunier *et al.* 2024). Non-farm factors include social norms (Villamayor-Tomas *et al.* 2019), social identity (Sulemana & James 2014), social capitals (de Krom 2017), communication mechanisms (Breetz *et al.* 2005), and other stakeholders in the socio-ecosystem (Brinks & de Kool 2006; Dessart *et al.* 2019; Meunier *et al.* 2024). The interactions among these factors are complex and challenging to fully comprehend, particularly in how they collectively influence farmers' behavior (Ren *et al.* 2022; Li *et al.* 2024). However, individual studies focusing on specific aspects of farmers' behavior have provided critical insights into the relationships between these factors. These findings will be examined in detail in the following sections.

Farm-related factors

Traditional plant protection practices typically involve the use of synthetic pesticides, which are associated with well-documented health risks (Damalas & Eleftherohorinos 2011). Consequently, health and well-being concerns are key factors influencing the adoption of SPPAs, which pose lower health risks. Vegetable farmers in Bangladesh perform unsafe pesticide practices due to a lack of awareness of the links between pesticide use and non-communicable diseases (Shahidullah *et al.* 2023). Health motivation was also among the key factors in promoting green pesticide use by Iranian farmers (Ataei *et al.* 2021).

Besides health-related risks, there are many other risks associated with crop production (Duong *et al.* 2019). The perception of these risks of individual farmers influences their adoption of SPPAs. For example, farmers' perception of environmental risks is a key factor in the adoption of SPPAs in Switzerland. Those who view pesticide use as significantly harmful to the environment and human health are more likely to adopt pesticide-free practices. Notably, concerns about environmental impacts- such as the long-term effects on soil health and biodiversity- often outweigh health-related considerations in influencing their decision-making (Finger & Möhring 2022). Risk perception is defined as a farmer's evaluation of the likelihood that specific risks will impact their business, as well as the potential consequences of those risks (Gardebroek 2006). These risks are perceived differently across regions, with low- and middle-income countries often concerned more about weather-related risks, while biosecurity (pest and disease outbreak, invasive species, etc.) was more frequently noted in developed nations (Duong *et al.* 2019). However, it is important to recognize that weather-related and pest-related risks are inherently interconnected (Mattson & Haack 1987; Peng *et al.* 2020). Weather events, such as extreme storms, droughts, or floods, not only pose immediate threats to crop yields but also increase the likelihood and severity of pest and disease outbreaks (Mattson & Haack 1987; Risch 1987). Furthermore, such events may create conditions conducive to the establishment and spread of invasive species, highlighting the inextricable link between climatic and biosecurity risks for farmers in all regions (Diez *et al.* 2012).

Farmers' socioeconomic backgrounds, including education, farm size, and experience, influence their risk perception, affecting their adoption of various risk management strategies, including SPPAs (Duong *et al.* 2019; Nastis *et al.* 2019). Particularly important is the role of economic factors, such as land ownership and investment behavior, in influencing environmental risk perception and the adoption of SPPAs, such as organic farming programs (Toma & Mathijs 2007). Similar findings were reported in many studies which found that

farmer's interest in participating in SPPAs due to environmental risk is often influenced by their economic factors (Wilson & Hart 2000). Economic factors, such as farm size and income, also influence the ability to process and utilize information, which is usually positively correlated with the perceived environmental risks of using pesticides (Tucker & Napier 2001). While education can enhance cognitive capacity and exposure to risk-related information, it is not directly influenced by economic factors as implied in this study.

Risk attitude refers to a farmer's perspective on risk and its implications, encompassing a spectrum from caution (risk-averse) to indifference (risk-neutral) to a propensity for risk-taking (Gardebroek 2006). A critical element of this is risk tolerance, which significantly influences a farmer's willingness to adopt sustainable practices. Generally, risk-averse farmers, who often face income volatility, high debt, and low profit margins, may perceive financial risks in adopting innovative, sustainable methods. These risks stem not only from the potential upfront costs of SPPAs but also from concerns about their lower efficiency compared to synthetic pesticides under conditions where pesticide resistance is not yet a significant issue. For example, Mkenda *et al.* (2015) demonstrated that synthetic pesticides like Karate are highly effective at controlling pests, often outperforming plant-based alternatives in immediate pest reduction. Similarly, Klonsky (2012) found synthetic pesticides more effective and less labor-intensive than organic methods, especially for labor-intensive crops like strawberries. While SPPAs can support pest control and ecosystem services, their perceived costs and labor demands may deter adoption without stronger incentives or evidence of long-term benefits. In contrast, risk-tolerant farmers, who are more accepting of uncertainties, tend to adopt innovations such as organic farming more readily (Dessart *et al.* 2019). Research focusing on small-scale farmers indicates that risk tolerance is shaped by various factors, including experience, education, farming income, access to capital, land ownership, and land size (Agussabti *et al.* 2020).

One of the most important factors influencing the adoption of SPPAs is how well farmers understand the risks and benefits of particular SPPAs, namely literacy regarding SPPAs. For instance, pesticide application knowledge, including the associated behavioral skills, can promote SPPAs (Li *et al.* 2023). Farmers with higher education were more likely to recognize both the pros and cons of pesticides and showed greater support for adopting biological control methods in Iranian (Abdollahzadeh *et al.* 2015). Higher literacy leads to safer pesticide use in Nepal, with men being more informed than women (Atreya 2007). In Bangladesh, educated watermelon farmers are more likely to adopt SPPAs. Education increases awareness of agrochemical risks and the benefits of sustainable practices, making it a key factor in promoting the transition to organic methods (Hoque *et al.* 2022). Similarly, the educational level significantly influences farmers' pesticide use against mosquitoes in rural farmers in Côte d'Ivoire (Kouame *et al.* 2022). Low levels of education and lack of proper training can lead to unsustainable use of pesticides in some regions due to the focus on maximizing profits. Many farmers are unaware of pesticide risks or fail to adopt protective measures, prioritizing higher yields over safety and environmental concerns (Akter *et al.* 2018).

The adoption of SPPAs by farmers is significantly influenced by their perceived behavioral control. This concept encompasses their confidence in their ability to successfully implement these approaches and their belief in their capacity to overcome potential barriers. Higher perceived behavioral control is associated with stronger intentions to engage in such practices, as it reflects both their self-efficacy and the availability of external resources and support necessary for execution (Albarracín *et al.* 2024). In Vietnam, farmers who feel confident in their ability to implement SPPA practices are more likely to adopt them, while so-

cial pressures or expectations (i.e., subjective norms) have little impact on their decisions. Younger farmers are more inclined to adopt SPPAs than older farmers, who often lack confidence in their ability to make the transition. This highlights the importance of improving farmers' perceived control through targeted policies and educational programs to promote the wider adoption of sustainable practices (Phung & Dao 2024). A similar phenomenon was observed among Swiss fruit farmers, where the belief in their ability to influence future outcomes played a critical role in their adoption of preventive pest management measures (Knapp *et al.* 2021).

The personality of the farmer is known to influence farmers' behavior. Personality traits refer to distinctive patterns in how individuals think, feel, and behave (Bergner 2020). Traits such as extraversion, openness to new experiences, agreeableness, neuroticism, and conscientiousness can significantly influence a farmer's decision-making (Costa & McCrae 1992; Austin *et al.* 2001; Crase & Maybery 2004). Traits such as openness and agreeableness are crucial in determining how farmers adopt best practices for managing remnant bush and revegetation in Australia (Crase & Maybery 2004).

Trust is a multidimensional construct encompassing personal trust (farmers' belief in the individual advisor), relational trust (farmers' perception that the advisor understands and respects their goals), and institutional trust (farmers' confidence in the formal source of the message, such as public, private, or charitable institutions) (Sutherland *et al.* 2013). Several studies have demonstrated the impact of institutional trust- confidence in the fairness and reliability of organizations- on achieving behavioral change and adoption of SPPAs through advisory services (Sutherland *et al.* 2013; Barghusen *et al.* 2021; Pierrette Coulibaly *et al.* 2021; Albarracín *et al.* 2024; Meunier *et al.* 2024). It was found that in some cases, the longevity and expertise of a service provider are more important for building relational trust than whether the advisory service is public, private, or charitable (Sutherland *et al.* 2013). Farmers in two contrasting European countries (Hungary and the UK) were found to place trust in sources whom they perceived as empathetic towards their needs (Rust *et al.* 2022). Another case in China (Hebei cotton) concluded the use of SPPAs is influenced jointly by information provision and trust (Jin *et al.* 2015).

Farmer typologies, which classify farmers based on shared characteristics such as resource endowments, priorities, and production strategies, can significantly influence the adoption of SPPAs (Van der Ploeg *et al.* 2009). The adoption of SPPAs by farmers from Hainan, China, is significantly associated with their capital endowments (Xu *et al.* 2023), which refers to the capability and resources a farmer household has to support production and livelihood. Indicators of capital endowments include natural capital (e.g., farmland area), economic capital (e.g., household income), human capital (e.g., number of labor force, health status), and social capital (e.g., interpersonal interaction, communication, and institutional trust) (Xu *et al.* 2023). Farmers that prioritized yields were less likely to support SPPAs, as they perceived more benefits from pesticide use in boosting productivity in Iran (Abdollahzadeh *et al.* 2015). Larger, wealthier farms with more access to resources are often more capable of adopting sustainable practices due to their ability to absorb risks and manage the upfront costs of implementation. In contrast, small-scale farms may struggle to adopt such practices due to limited capital and higher perceived risks (Ren *et al.* 2019). Off-farm income, often viewed as a risk management strategy against whole-farm risk, plays a crucial role in facilitating the adoption of SPPAs, as farmers with such income sources tend to be more willing to take on the perceived risks associated with implementing these practices (Sharifzadeh *et al.* 2018). Moreover, using one risk management strategy can trigger the adoption of another, highlighting the interactive nature of risk management approaches. Additionally, farms that produce high-value or export-oriented crops are more likely to adopt

sustainable methods driven by market incentives and regulatory pressures (Peeters *et al.* 2015).

Although not directly related to plant protection practices, some cases illustrate that farmers' relationships with nature play a crucial role in shaping their sustainable agricultural practices. For example, farmers in the US Midwest, particularly in two Illinois watersheds, are instrumental in managing nitrogen fertilizers and addressing water quality issues (Yoshida *et al.* 2018). Surveys and interviews revealed a spectrum of perspectives: while some farmers adopt a "Master" view, attributing environmental problems to human activity, many embrace a stewardship or partnership ethos with nature, which drives their conservation efforts. However, despite these ecological values, production pressures, livelihood concerns, and systemic challenges often constrain their ability to fully implement conservation practices (Yoshida *et al.* 2018). This finding highlights the multifaceted human–nature relationships underlying agricultural decisions, with critical implications for resource management, conservation efforts, and environmental sustainability.

Non-farm factors

Studies looking at farmer's use of SPPAs have identified that non-farm drivers as a common driver toward SPPAs (Rogers *et al.* 2023). Starting from the more local factors, farmers' behavior associated with SPPAs is often influenced by social capital (Bhandari & Yasunobu 2009). Social capital refers to the networks, relationships, and norms that facilitate collective action within a society. Broadly, it is understood as a collective resource composed of shared values, beliefs, trust, social relationships, and institutions that enable cooperation and collective action for mutual benefit (Bhandari & Yasunobu 2009). Factors associated with social capital include the status of the farm, the frequency with which farmers share information with others, whether farmers are involved in agricultural associations, and whether they are influenced by the business behaviors of others. While not directly linked to SPPAs, behaviors related to sustainable fertilizer use, such as fertilizer reduction, have been found to correlate strongly with social capital (Zheng *et al.* 2022). The impact of social capital, such as communication among farmers, is highest for part-time farmers, followed by large-scale professional full-time farmers, and lowest for small-scale full-time farmers (Zheng *et al.* 2022). This suggests that social capital may also interact closely with farm status to influence the adoption of SPPAs.

The interactions among farms and other stakeholders contribute to the development of specific social norms. A social norm refers to unwritten rules that guide behavior in society based on what is commonly done or believed to be appropriate (Albarracín *et al.* 2024). An injunctive norm specifically refers to the perception of what behaviors are approved or disapproved of by others, focusing on moral expectations. It reflects the social pressure to conform to behaviors that are seen as "right" or "wrong," such as feeling the need to recycle because it is widely viewed as the correct action in a community. These norms play an important role in facilitating the adoption of SPPAs. For example, peer influence and the behavior of neighboring farmers significantly impacted smallholder farmers' decisions in Cambodia to adopt sustainable pest control methods, such as setting aside land to support natural enemies (Bell *et al.* 2016). A similar pattern was observed among Iranian farmers, where social norms positively influenced their intention to use green pesticides (Ataei *et al.* 2021). In developed countries, evidence suggests similar dynamics. For instance, European farmers' participation in agri-environmental schemes was shaped by peer orientation and social norms, even within robust institutional frameworks (Bartkowski & Bartke 2018). However, while these factors are important, their influence remains understudied, particularly in developed settings, highlighting a need for further research to optimize governance strategies leveraging social dynamics.

One key factor that facilitates the adop-

tion of SPPAs is governmental subsidies or financial support. In Cambodia, financial incentives for maintaining non-crop habitats encouraged farmers to collaborate and adopt SPPAs, helping to overcome coordination challenges and mitigate the risk of free riders (Bell *et al.* 2016). While this study does not directly demonstrate an increase in SPPA adoption, research shows that government fiscal expenditure on agriculture is positively associated with sustainable agricultural economic development (Zhang & Zhang 2024). This suggests that government support enhances the overall value of sustainable agriculture, which likely reflects improved implementation of SPPAs (Zhang & Zhang 2024). Subsidies can be effective, but their impact likely varies depending on program design and local conditions, highlighting the need for further evaluation.

Markets play a significant role in increasing the adoption of sustainable agricultural practices (Stavins 1989; Grabosky 1994), particularly in plant protection. Market forces, such as consumer preferences, regulatory requirements, and financial incentives, drive businesses to adopt environmentally friendly practices. In plant protection, these forces encourage the implementation of integrated pest management (IPM) and reduced pesticide use as markets and consumers increasingly favor products with lower environmental impacts. Financial institutions and private-sector collaborations reinforce these efforts by rewarding compliance with environmental standards. The rise of environmental, social, and governance (ESG) criteria has further incentivized farmers to adopt SPPAs, as financial benefits and market access increasingly depend on meeting these standards. Investor and stakeholder pressure has made ESG integration a necessity for managing risks and enhancing competitiveness. This trend aligns environmental sustainability with economic incentives, fostering broader adoption of sustainable practices (Zaccone & Pedrini 2020). Additionally, growing consumer demand for sustainability pressures agricultural producers to innovate and adopt green technologies, including safer and more sustainable plant protection methods (Grabosky 1994; Codron *et al.* 2014; Martins *et al.* 2025). The relationship between farmers and buyers plays a significant role in the adoption of SPPAs. Farmers with formal contracts with lead companies- often including provisions such as quality standards and technical support- are much more likely to adopt SPPAs, as seen in Chile's vegetable sector. In contrast, farmers relying on informal agreements, particularly with intermediaries, are less likely to implement these sustainable practices. This research highlights the critical role formal contracts play in encouraging the adoption of environmentally friendly farming methods (Benitez-Altuna *et al.* 2023). Market influence on the adoption of SPPAs is particularly obvious in export-driven sectors. In the case of fresh tomato production in Morocco and Turkey, private market regulations and the safety demands of importing countries are the primary drivers of practices like IPM and good agricultural practices (GAP). Moroccan growers, exposed to stringent European Union safety standards, show higher adoption rates of IPM and GAP due to strong vertical integration in supply chains and collective compliance efforts. Conversely, Turkish growers have lower adoption rates, largely influenced by weaker safety requirements in traditional export markets and less developed private regulatory systems (Codron *et al.* 2014).

The adoption of SPPAs by farmers is significantly influenced by market demand and consumer trust in green products. Wang *et al.* (2024) demonstrate that increased consumer preference for high-quality, environmentally friendly products raises market prices and trust, creating economic incentives for farmers. These market-driven incentives are amplified by the government's regulatory efforts and ecological subsidies. While subsidies and stable market prices for green products help offset production costs and risks, they complement rather than substitute market demand. As the study illustrates, market demand alone may not always outweigh other barriers, such as farmers'

skepticism or high production costs. Instead, a dynamic interplay between consumer demand, government support, and market regulations fosters a stable equilibrium, promoting the adoption of SPPAs (Wang *et al.* 2024). The agricultural product market is not the only market influencing the adoption of SPPAs; other markets, such as the land market, can also have an indirect impact (Shen & Wang 2024). A study in China found that market-oriented land allocation- driven by rural-to-urban migration and resulting in larger farm sizes- promoted cropland quality protection activities, including greater adoption of SPPAs. This is believed to be linked to increased farm size and higher agricultural income (Shen & Wang 2024).

STAKEHOLDERS AND FARMERS' ADOPTION OF SPPAS

Farmers' engagement in SPPAs is significantly impacted by their interactions with various stakeholders, including farmers, public, and private sectors (Scherfranz *et al.* 2024). While we recognize that these stakeholders could also be categorized as non-farm factors, in this section, we aim to focus more on the interactions between these actors. This section provides a different perspective discussing how different factors influence the adoption of SPPAs. As mentioned before, the market exerts a strong influence on the adoption of SPPAs, and buyers can, therefore, influence the adoption of SPPAs. In the Chile example, farmers involved in informal contracts were less likely to adopt SPPAs (Benitez-Altuna *et al.* 2023). Nestle's production standards in Yunnan can facilitate the use of SPPAs (Rogers *et al.* 2023). Agribusiness can, therefore, have a positive impact on the adoption of SPPAs. On the other hand, industry influence can also be a barrier to the adoption of SPPAs. A study on cashew farms in Ghana found a different trend: farmers with a strong inclination towards contract farming showed lower probabilities of using sustainable agricultural practices, possibly due to the inputs of fertilizers and pesticides provided by contracting companies (Dubbert *et al.* 2021). In the cases of Tunisian olive oil companies, the commitment to implementing environmentally friendly actions (rationalization of water consumption, reduction of pesticides and insecticides) remains largely compliance-based, with minimal financial or technical support from dominant firms, limiting the extent of environmental improvements (Achabou *et al.* 2017). This may reflect that the market has not yet shifted significantly toward a demand for 'green products,' reducing the incentive for industries to adopt sustainable practices. Alternatively, it could suggest that industries underestimate the growing consumer interest in sustainability. Either way, the misalignment between market trends and industry actions presents a significant barrier to the broader adoption of sustainable practices. Agricultural advisory services linked to agribusinesses can raise concerns about conflicts of interest. For example, in China, advisors connected to agribusinesses recommend pesticides 18% more often than independent advisors (Wan *et al.* 2019). Similarly, in Brazil, 40% of the support farmers receive comes from vendors of fertilizers and agrochemicals, raising questions about the objectivity of the advice provided. Additionally, lobbying by farming organizations that prioritize their own benefits over sustainability has been identified as another barrier to promoting sustainable practices (Latawiec *et al.* 2017).

Governments can influence the change in farming practices through policy (David *et al.* 2022). Government subsidies are a strong motivator of SPPAs, especially regarding sustainable pesticide application behavior (Li *et al.* 2023; Xiang & Gao 2023). While subsidies effectively promote SPPA adoption, penalties also drive sustainable practices. Penalties, when strictly enforced, deter harmful activities and encourage compliance by increasing the economic costs of unsustainable behaviors (Zhou & Han 2024). They also motivate farm-

ers to adopt environmentally friendly practices, such as straw return, by creating disincentives for non-compliance and reinforcing community norms (He *et al.* 2023). With subsidies and education, penalties form a comprehensive policy framework to ensure widespread SPPA adoption. Other policies and incentives such as training, public awareness campaigns, field demonstrations and workshops can help to encourage SPPA adoption by educating and changing farmers' perception of their ability to perform a practice (Phung & Dao 2024). On the other hand, institutional failures such as corruption, non-transparent governance structures, or unclear governance structures act as a barrier (Martin *et al.* 2015; David *et al.* 2022). However, this has mostly been reported in low- and middle-income countries.

Farmer-specialized cooperatives are an important player in the interactions between farmers and the government. The interactions between the government, farmer cooperatives, and individual farmers will influence the simulated progression of decision making among the three parties (Teng *et al.* 2022). The government's regulatory measures and incentives (like rewards and penalties) encourage cooperatives to manage farmers' production practices effectively. Cooperatives play a crucial role by supervising farmers, offering training, and providing financial incentives to adopt SPPAs (Teng *et al.* 2022). A notable case from the Wufeng District Farmers' Association in Taichung, Taiwan, shows how contractual price guarantees, input provision, collective pest management, and corporate sponsorship expanded environmentally friendly contract farming to nearly 58 hectares in five years (Yen & Chen 2021). Thus, cooperatives are vital in promoting SPPA adoption and linking policy to farmer behavior.

Extension services provided by experts played a key role in raising awareness about the negative effects of pesticides and providing the technical knowledge needed to implement sustainable pest management strategies (Wuepper *et al.* 2021). Farmers with frequent contact with extension agents were significantly more likely to adopt biological control methods in Iran (Abdollahzadeh *et al.* 2015). However, many farmers increasingly rely on peer networks and social media rather than traditional agricultural experts for advice on sustainable soil management. Farmers, particularly in the UK and Hungary, expressed greater trust in other farmers, valuing practical, firsthand knowledge over academic or governmental expertise. This shift is driven by a perception that experts often lack a deep understanding of the farmers' real-world challenges. The growing use of farmer-to-farmer interactions and social media highlights a significant change in how agricultural decisions are made, with peer networks becoming a more influential source of information (Rust *et al.* 2022). For example, In Taiwan, nearly 70% of strawberry farmers regularly exchange information with peers, discussing pest and disease outbreaks, control strategies, and pesticide use across all age groups (Huang *et al.* 2022). However, the ease of sharing on social media also facilitates the spread of misinformation, undermining trust and delaying science-based practices. Strengthening information literacy and fact-checking mechanisms is essential to mitigate these risks (Chowdhury *et al.* 2023).

These observations align with the findings that farmers' adoption of practice changes can be significantly influenced by peers, as individuals often align their behavior with perceived social norms (Michel-Guillou & Moser 2006). For instance, a case study in Cambodia concluded that decisions to increase the use of non-crop habitats for natural enemies are more influenced by the farmer's social environment (Bell *et al.* 2016). Similarly, French wine growers that participate in management schemes were driven by the perceived involvement of their peers (Kuhfuss *et al.* 2016). Moreover, studies on UK farmers, underscore the significant impact of peers on the adoption of SPPAs (Mills *et al.* 2017; Oerlemans & Assouline 2004).

Additionally, non-governmental organi-

zations (NGOs) also play a variety of roles in advancing the adoption of SPPAs, including bridging information gaps, participating in public decision-making, accessing markets, and shaping legislative frameworks. A case study of small-scale farms in Nicaragua suggests that the efficacy of NGOs in facilitating the adoption of SPPAs may be enhanced if NGOs employ a non-centrist approach, which means a more bottom-up, two-directional relationship, collaborating closely with local stakeholders, engage in mutual learning and teaching as they collectively advance toward solutions for their social challenges (Dyck & Silvestre 2019). A case study in Taiwan highlights an NGO's use of the participatory guarantee system (PGS)- a community-based, locally driven alternative to third-party certification- to promote environmentally friendly farming. By involving producers, consumers, and other stakeholders in joint farm visits and decision-making, PGS fosters trust, transparency, and shared learning. Over six years, this approach expanded eco-friendly farming from 3.3 to 284 hectares, demonstrating its potential to advance the adoption of SPPAs (Chen *et al.* 2018; Lo 2024).

There are notable differences in how relationships between public and private sectors and farmers influence the adoption of SPPAs, often leading to contrasting outcomes. In Switzerland, farmers receiving advice from private companies are 9–10% more likely to rely on synthetic pesticides for pest management compared to those advised by public extension services (Wuepper *et al.* 2021). In contrast, farmers advised by public extension workers are more likely to adopt preventative pest control measures. Furthermore, when farmers receive advice from multiple public extension services (e.g., different organizations), the likelihood of adopting preventative measures increases (Wuepper *et al.* 2021). In China, the adoption of sustainable agrochemicals, such as those used by coffee farmers in Yunnan and orange farmers in Hubei, is shaped by interactions between public and private sector advisory services. However, the primary leadership often depends on the context: For instance, in Yunnan, agribusinesses like Nestlé play a leading role by providing inputs, training, and certification standards, while in Hubei, local government initiatives promote organic fertilizers to address environmental goals. This highlights the need for coordination between sectors to optimize adoption and sustainability outcomes (Rogers *et al.* 2023).

CHALLENGES TO PROMOTING SPPAS

The adoption of sustainable farming practices is often hindered by several key challenges. High costs, lack of financial support, ineffective information dissemination, weak institutional frameworks, and limited stakeholder collaboration are among the key hurdles for adopting SPPAs. Addressing these challenges is essential to promoting sustainable farming on a global scale (David *et al.* 2022).

Farmers are often slow to shift to adopt SPPAs due to concerns about the costs involved, pest pressure, and the lack of effectiveness of SPPAs. Farmers often face economic pressures and prioritize profitability, making them more likely to rely on chemical controls rather than adopting SPPAs, such as biological control. Therefore, despite efforts like IPM and associated subsidies, there has been little reduction in overall pesticide use in California (Epstein & Bassein 2003). The perceived lack of effectiveness of SPPAs is closely linked to gaps in ecological knowledge. The comparative effectiveness of SPPAs versus conventional pest control methods is a critical criterion for many farmers (Sharifzadeh *et al.* 2018). A significant component of SPPAs involves the use of biological control agents (i.e., natural enemies of insect pests) to reduce pest populations. However, knowledge about biological control is often limited among some farmers. For example, Honduran farmers who predominantly rely on synthetic pesticides tend to

have low awareness of biological control, particularly regarding its potential effectiveness and proper implementation (Wyckhuys & Neil 2007). Kiwi farmers in China can perceive SPPAs as high-risk method and therefore choose not to adopt these measures (Xiang & Gao 2023).

Institutional failures further exacerbate these challenges by creating an unstable environment that discourages investment in SPPAs. Weak governance frameworks, corruption, and lack of regulatory enforcement undermine farmers' trust and willingness to engage in sustainable practices (Martin *et al.* 2015). In Malaysia's palm oil sector, for instance, smallholders face ambiguous land rights, making long-term investment in sustainable practices risky. Cases of land-grabbing and corruption often discourage farmers from adopting innovative approaches (Martin *et al.* 2015). Institutional voids also hinder access to resources such as technical knowledge, financial support, and market opportunities. Farmers operating in marginal regions often remain disconnected from global supply chains, limiting their awareness of sustainable practices and technologies. For example, Sabahan palm oil smallholders are reluctant to adopt sustainable practices due to poor infrastructure, lack of education, and weak institutional support systems (Martin *et al.* 2015). Additionally, there is a lack of proper extension infrastructure that effectively disseminates SPPAs knowledge to farmers. For example, in certain regions, lack of extension services leads to pesticide misuse which increases health risks and hinders the adoption of SPPAs (Ngowi *et al.* 2007). However, sometimes changing the mindset is not enough. In some cases, farmers are willing to adopt SPPAs, but their actual behavior might not match their willingness (Qiao *et al.* 2022). Factors such as education, social network, and age can have a major impact on the gap between farmers' expressed willingness to adopt SPPAs and their actual behavior (Qiao *et al.* 2022). This discrepancy may partly arise from social desirability bias, where individuals express socially acceptable intentions (e.g., willingness to adopt sustainable practices) that do not translate into action due to other underlying barriers, such as economic constraints or limited access to resources (Grimm 2010). Additionally, overcoming deeply ingrained traditional habits poses another challenge. In some regions, long-standing practices significantly contribute to unsustainable farming behaviors (Pirmoradi & Rostami 2021).

Establishing regulations for sustainable agricultural practices is an important strategy to promote the adoption of SPPAs. However, such regulations can sometimes inadvertently marginalize smallholder farmers and accelerate land transfers to larger-scale operations (Rogers *et al.* 2023). Additionally, the higher costs associated with implementing SPPAs present a significant barrier to their adoption, particularly for resource-limited farmers (Sharifzadeh *et al.* 2018; Li *et al.* 2023). Another example is the Food Quality Protection Act (FQPA) in California which successfully reduced the use of hazardous pesticides. However, this reduction primarily resulted in the substitution of older chemicals with newer ones, rather than promoting the adoption of SPPAs. The shift to alternative pesticides has not substantially advanced the use of non-chemical methods, and IPM programs have been effective only when they provide direct economic benefits to growers. Without such incentives, the adoption of SPPAs remains limited, emphasizing the need for more targeted and robust strategies to encourage sustainable practices (Epstein & Zhang 2018). Additionally, strict food safety standards designed to prevent contamination and ensure consumer safety can inadvertently discourage practices that promote ecological sustainability. For instance, these standards often require farmers to remove non-crop vegetation and wildlife habitats, practices that align with food safety but contradict biodiversity conservation efforts (Baur 2022). Similarly, concerns about microbial contamination may lead farmers to abandon organic soil amendments like compost in favor of synthetic fertilizers, which do not enhance ecosystem ser-

vices such as pest predation (Baur 2022). This regulatory emphasis on immediate food safety often takes precedence over long-term environmental goals, creating a significant barrier to the adoption of SPPAs. SPPAs, such as habitat conservation and integrated pest management, which are central to sustainability, rely on voluntary incentives and fragmented policies that lack the enforcement mechanisms and consistency of food safety regulations. Furthermore, market-driven pressures to comply with strict food safety standards reinforce this prioritization, leaving farmers with limited flexibility to implement sustainability-focused practices (Baur 2022).

Systems or policies designed to promote the adoption of SPPAs do not always achieve their intended outcomes. For instance, while the division of labor is often predicted to enhance efficiency, and outsourcing services theoretically could improve resource utilization and facilitate SPPA adoption, the reality can differ. In China, pesticide outsourcing services provided by organizations or professional cooperatives, originally intended to promote sustainable practices by reducing synthetic pesticide use, have instead led to increased herbicide application and reduced manual weeding (Yang *et al.* 2023). The authors attribute this outcome to imperfections in the outsourcing service market, which shift farmers' practices from labor-intensive processes to capital-intensive ones, such as increased reliance on synthetic pesticides (Yang *et al.* 2023).

In addition to the public sector, the private sector plays a crucial role in promoting the adoption of SPPAs. Large companies can sometimes encourage sustainable practices; however, relying solely on them is not always an effective solution. Market forces, specifically participation in global value chains (GVCs), influence the adoption of SPPAs. GVCs involve production processes distributed across multiple countries, with firms in the Global South supplying components or raw materials while multinational corporations set production standards. For example, Tunisian olive oil companies have adopted SPPAs, such as reducing pesticide use, to comply with international market standards, particularly among export-oriented firms (Achabou *et al.* 2017). While compliance with organic certification has driven product upgrading, broader environmental challenges persist. One significant issue is the management of vegetable water, a byproduct of olive oil production. Improper disposal of vegetable water, which contains high pH levels, fatty substances, and oxygen-consuming organic content, can harm aquatic ecosystems. The volume of vegetable water generated depends on the processing method used. Modern techniques, such as two-phase centrifugation, significantly reduce waste compared to traditional methods. However, in countries like Tunisia, adopting these technologies is hindered by limited financial and technical resources. This example illustrates that while market demands can drive targeted improvements, such as pesticide reduction, addressing broader environmental challenges like pollution management requires more robust financial and technical support systems. The absence of collaborative assistance from dominant GVC actors limits the potential for comprehensive environmental upgrading (Achabou *et al.* 2017). Similarly, contract farming practices can also affect the adoption of SPPAs. Contract farmers in Ghana, particularly those engaged in agreements emphasizing productivity and input provision, rely more heavily on chemical inputs, leading to less sustainable practices compared to non-contract farmers. Contracts focusing on short-term yields often discourage the adoption of SPPAs, demonstrating the need for contract structures that align productivity goals with sustainable practices (Dubbert *et al.* 2021).

Most of these challenges have been identified through past research on farmers' behavior, primarily using correlation studies. However, studies that focus solely on correlations between factors and behavioral changes have been deemed insufficient for predicting the effectiveness of intervention measures designed to modify behavior (Albarracín *et al.* 2024). This limitation arises from findings that the

most effective factors for driving behavioral changes differ significantly between correlation-based studies and experimental intervention studies (Albarracín *et al.* 2024). For example, for the off-farm factors that are linked to behavior changes, correlation studies generally identified trustworthiness as the most important factor leading to behavior change while actually intervention studies have identified access to be the most important factor (Albarracín *et al.* 2024). Access refers to the ease with which the environment enables a given behavior to occur. For example, lowering the price of environmentally friendly pesticides would increase access to these SPPAs. These findings underscore the importance of prioritizing data from intervention studies to identify effective strategies for encouraging farmers to adopt SPPAs. Future research should focus on intervention-based approaches rather than solely on correlation studies exploring the links between factors and behaviors. Additionally, the influence of various factors on the adoption of SPPAs can change over time due to the dynamic nature of social, political, and economic environments (Li *et al.* 2023). This highlights the critical need for long-term studies to monitor and understand the factors driving farmers' behavior.

Oversimplifying farmers' motivations is likely a significant limitation in promoting the adoption of SPPAs. While financial incentives are undoubtedly critical, prioritizing immediate livelihood needs often poses a substantial hurdle to the adoption of SPPAs. Farmers facing economic precarity, particularly in the Global South, may focus on short-term productivity and income over long-term sustainability, even when financial incentives are available. While this reality highlights the potential of increasing financial incentives to encourage the adoption of SPPAs, the issue is far more complex. For instance, oversimplifying farmers' motivations has been suggested to be a significant issue that has hindered the environmental effectiveness of the European Union's Common Agricultural Policy (CAP), including the adoption of SPPAs. Despite substantial financial investments, the CAP has fallen short of achieving its biodiversity goals. Biodiversity is intrinsically linked to SPPAs, as practices like reduced pesticide use, integrated pest management, and biological control help preserve ecosystems by minimizing harm to non-target species, supporting natural pest control, and fostering pollinator populations. This failure stems from an overemphasis on economic incentives while neglecting the social and contextual factors that influence farmers' decisions. For instance, studies have shown that financial payments, when not paired with social and technical support, fail to overcome barriers such as limited resources, lack of trust, and contextual constraints (Brown *et al.* 2021).

SOLUTIONS FOR PROMOTING SPPAS

To encourage the broader adoption of SPPAs, addressing concerns about the potential costs and risks is essential. Policy measures such as financial incentives and education programs can play a crucial role in encouraging broader adoption of sustainable farming practices. One effective strategy to reduce the concerns and psychological barriers associated with SPPA adoptions is the establishment of crop insurance systems. Research has shown that crop insurance can reduce synthetic pesticide use by up to 33% (Li *et al.* 2022), demonstrating its potential to promote sustainable practices. For risk-averse farmers, targeted policies should prioritize reducing financial uncertainties. For instance, initiatives like insurance schemes tailored to SPPA adoption, financial incentives, or income-stabilizing subsidies all serve to stabilize farmers' incomes, thereby reducing the perceived risks associated with adopting SPPAs (Guo *et al.* 2021). For example, farmers who adopt SPPAs could qualify for lower insurance premiums or receive higher indemnities. Specific measures could include offering reduced insurance pre-

miums or higher indemnities to farmers who adopt SPPAs, providing a tangible economic benefit that offsets the potential costs. By alleviating financial concerns, these approaches might facilitate the transition to sustainable farming practices while addressing farmers' apprehensions about economic stability. However, insurance does not always promote the adoption of SPPAs, as research indicates that crop insurance may sometimes have unintended consequences, such as increased pesticide use. Studies have shown that insurance can incentivize farmers to adopt more pesticide-intensive farming practices, particularly by encouraging the cultivation of high-risk, high-input crops and increasing pesticide use per hectare (Möhring *et al.* 2020). This occurs because the financial safety net provided by insurance reduces the economic risks of crop failure, making farmers more likely to invest in intensive agricultural practices. To ensure that insurance aligns with the goals of SPPAs, policy frameworks should incorporate conditions or incentives that explicitly encourage sustainable practices. For instance, insurance schemes could be linked to IPM or organic certification, offering reduced premiums or additional coverage for farmers who minimize synthetic pesticide use. Similarly, combining insurance programs with education and technical support for SPPAs can help farmers adopt risk-reducing sustainable practices without compromising productivity or profitability. By addressing these complexities, insurance policies can be designed to both mitigate risks and promote environmentally sustainable farming systems.

To improve farmers' risk tolerance- whether by influencing risk attitudes or building resilience- strategies should emphasize enhancing educational programs, engaging key stakeholders, fostering networking opportunities, promoting cluster-based approaches, and utilizing technology. These efforts can help shift perceptions, build confidence, and empower farmers to better manage risks in their operations (Agussabti *et al.* 2020). Additionally, the perceived lack of effectiveness in SPPAs is often due to a lack of knowledge and confidence in their implementation. To address this, it is crucial to expand training programs that equip farmers with the necessary knowledge and skills. This is especially important because behavioral skill training has been identified as a moderately effective approach for driving behavior change (Albarracín *et al.* 2024).

A recurring theme in the literature is the role of literacy and education as both a factor influencing the adoption of SPPAs and a challenge limiting their adoption. The transfer of knowledge from researchers or government agencies to farmers relies heavily on extension workers. Therefore, establishing effective extension systems is essential to educate farmers about different types of SPPAs. For example, in Honduras, farmers with greater knowledge of biological control were more likely to adopt environmentally friendly pest control approaches (Wyckhuys & Neil 2007). Local meetings, training, and public awareness campaigns are also important activities that enhance knowledge and motivation among farmers to promote sustainable practices (Ataei *et al.* 2021). Interestingly, in some regions, the longevity and expertise of a service provider have been identified as more important for building trust than whether the advisory service is public, private, or charitable (Sutherland *et al.* 2013). Consistent funding for well-established agencies or their affiliates is, therefore, more effective in influencing farmer behavior in the short term compared to short-term "contract" advisory projects involving inexperienced service providers (Sutherland *et al.* 2013).

In addition to knowledge dissemination by extension workers, farmer-to-farmer interactions are increasingly recognized as playing a crucial role in spreading knowledge (Rogers *et al.* 2023). In Taiwan, 70% of farmers seek advice from fellow farmers, 60% consult agricultural supply stores, 30% turn to research and extension stations, and fewer than 10% rely on farmers' associations (Huang *et al.* 2022).

Social media, for instance, has become a common channel for information sharing between farmers (Rogers *et al.* 2023). While not directly related to pest control, studies on water-saving behaviors offer insights that could inform strategies for promoting SPPAs. For example, a study in France found that social comparison nudges- such as sharing individual water use records with a community of farmers- reduced excessive irrigation among those using the most water and increased irrigation among those who did not irrigate at all. This intervention, facilitated by smart irrigation meters, proved to be a low-cost and effective method to change farmers' behaviors (Chabé-Ferret *et al.* 2019). Such social comparison nudges, along with farmer-to-farmer interactions, should be incorporated into the design of extension systems to facilitate the adoption of SPPAs better.

As discussed in previous sections, certain policies aimed at promoting SPPAs have, at times, led to undesirable outcomes. To avoid repeating these mistakes, it is essential to leverage current knowledge and design evidence-based strategies. Recent studies have identified that one of the most significant factors driving behavioral change is access to resources that facilitate the adoption of specific practices. Access encompasses the availability, affordability, and logistical ease of utilizing resources, such as providing necessary tools, reducing financial barriers, and ensuring convenient infrastructure. By removing environmental constraints, access creates tangible opportunities for individuals to act on their intentions and adopt desired behaviors effectively (Albarracín *et al.* 2024). For environmentally friendly behaviors, increasing access has the greatest impact on behavior change, followed by enhancing social support and improving behavioral skills. A promising example of an initiative that could address these factors is Taiwan's "Plant Doctor" system (McGovern & To-Anun 2016). This system equips farmers with essential technical knowledge and skills they may lack, increasing their capacity to adopt sustainable practices. By outsourcing SPPA-related services to organizations or extension workers like plant doctors, accessibility can be improved while also providing third-party certification for health and environmental stewardship. When combined with financial support or subsidies from the government, such initiatives could further facilitate the adoption of SPPAs by ensuring farmers have both the resources and guidance they need. However, a 2019 survey shows limited engagement across age groups- only 29% of farmers aged 31–40 and 18% of those aged 41–50 consult plant doctors, with no participation among those over 50 (Huang *et al.* 2022). This suggests the system's impact is uneven and requires further evaluation. Future research should evaluate its potential to enhance accessibility and foster sustainable agricultural practices. In addition to access, other factors, such as beliefs, behavioral attitudes, knowledge, administrative sanctions, and material incentives, appear to have a comparatively limited effect (Albarracín *et al.* 2024). The higher cost of SPPAs is a strong inhibitor of the adoption of these more environmentally sustainable plant protection approaches (Sharifzadeh *et al.* 2018; Li *et al.* 2023). Therefore, increasing subsidies for green pesticides and identifying additional strategies to boost farmer household incomes will be essential ways to improve accessibility and enhance the use of SPPAs (Li *et al.* 2023).

In addition, adopting SPPAs can be viewed as a health-promoting behavior for farmers. It is, therefore, important to approach these behaviors from a health perspective. Research suggests that the key factors influencing health-related behavioral changes include access, habits, material incentives, and descriptive norms (Albarracín *et al.* 2024). This indicates that when designing strategies to promote the adoption of SPPAs, it is important to understand whether farmers view SPPAs primarily as environmentally friendly practices or health-promoting behaviors. The framing of SPPAs can influence the most effective targets for behavior change.

Researchers and policymakers should avoid oversimplifying farmers' motivations and practices (Brown *et al.* 2021). Farmers possess valuable local knowledge and methods for protecting crops, and dismissing their knowledge or labeling them as ignorant does little to foster a better understanding of their behavior (Rogers *et al.* 2023). For instance, the European Union's CAP, which aims to promote sustainable practices, has faced challenges due to an oversimplified view of farmers' motivations. This has led to undesirable outcomes, as the policy relies heavily on economic incentives while neglecting the social and contextual factors that influence farmers' decisions. To improve its effectiveness, policies must consider the diverse and complex motivations that drive farmers to adopt environmentally sustainable practices. Farmers' adoption of sustainable crop protection practices is strongly influenced by behavioral factors, including time preferences and social influence. Farmers who heavily prioritize immediate rewards over future benefits are less likely to adopt practices that require upfront effort but provide long-term advantages (Albarracín *et al.* 2024). Social influence plays a crucial role in the adoption of sustainable practices, as farmers are more likely to adopt these methods when their peers do, but they may resist if their community is hesitant to change. This dynamic highlights a potential conflict between government policies that promote sustainable practices and the network effects within farming communities. While government policies may provide financial or technical incentives, the collective attitudes and behaviors of farming networks can either amplify or hinder their effectiveness. These behavioral factors, though often overlooked, are critical to ensuring that sustainable practices are widely and effectively adopted (Finger *et al.* 2024).

CONCLUSION AND FUTURE DIRECTIONS

The current agricultural system is heavily influenced by a Western industrialized perspective, prioritizing productivity over sustainability, often at great environmental cost (Ilbery & Bowler 2014). Conventional, intensive plant protection practices are particularly widely documented as key contributors to agriculture's negative impact on sustainability (Matthews 2018). To address this, it is essential to reform agricultural practices, particularly pest and pathogen management, by promoting the adoption of SPPAs as a crucial step toward a sustainable system.

However, changing farmers' behavior remains challenging, as crop production is both a livelihood and a primary source of income, with productivity and crop quality directly tied to financial stability. This focus on productivity often comes at the expense of sustainability. Researchers and governments must lead in promoting SPPAs by identifying and addressing the key factors influencing behavioral change, ultimately encouraging widespread adoption of sustainable practices.

We have identified various farm-related and non-farm factors that influence the adoption of SPPAs (Fig. 1). Farm-related factors include concerns about health risks associated with traditional plant protection methods (e.g., synthetic pesticides), risks related to productivity and costs, farmers' attitudes toward these risks, their knowledge or literacy about SPPAs, perceived behavioral control, personality traits, trust levels, and farm typologies. Non-farm factors encompass social capital, interactions with stakeholders, government financial support and subsidies, and market and consumer dynamics. Among these, interactions with different stakeholders in the agricultural system play a crucial role. For example, buyers significantly influence SPPA adoption, particularly when they impose regulations requiring specific plant protection practices, effectively compelling farmers to adopt SPPAs. Understanding the flow of capital, materials, and power within the agrochemical industry is crucial for uncovering how agribusinesses influence the adoption of SPPAs (Rogers *et al.* 2023). Equally important is preventing the marginalization of smallholders in deci-

sion-making processes dominated by large-scale agrochemical agendas, as many smallholders lack access to alternative pest control technologies (Rogers *et al.* 2023).

Governments and farm cooperatives also play a significant role in shaping SPPA adoption- sometimes encouraging it, but at other times inadvertently hindering it. It is essential to examine the network of government policies related to food safety, sustainability, and pollution control to understand how these interconnected policies impact the use of SPPAs (Rogers *et al.* 2023). For instance, food safety standards often conflict with sustainability by requiring habitat removal and discouraging organic amendments, which harms biodiversity (Baur 2022). Similarly, regulations like California's FQPA reduced hazardous pesticides but favored chemical substitutions over non-chemical methods, limiting SPPA adoption (Epstein & Zhang 2018). Addressing these challenges requires systemic reforms that align sustainability and food safety goals. Such reforms must be supported by coherent policies and incentives that empower farmers to adopt sustainable plant protection strategies (Baur 2022).

Farmer-to-farmer interaction is a key factor influencing the adoption of SPPAs, as demonstrated in various cases. Additionally, NGOs can play a significant role in promoting sustainable practices. For instance, in Nicaragua, an NGO successfully encouraged the adoption of conservation agriculture among small-scale farmers by using a bottom-up approach. This method prioritized local experimentation, two-way knowledge exchange, and farmer-led innovation, focusing on collaboration and capacity building rather than rigid, top-down standards. This approach proved highly effective, showcasing the potential for sustainable and lasting change (Dyck & Silvestre 2019).

However, these same factors can sometimes pose challenges to SPPA adoption. Farmers' traditions can be resistant to change due to farm-related characteristics such as risk tolerance, perceptions, and knowledge gaps. Additionally, the absence of effective extension systems and knowledge dissemination pathways often hinder SPPA adoption. The complexity of factors influencing farmers' behavior means that well-intentioned policies and regulations can sometimes have unintended negative consequences, reducing SPPA adoption rates.

The private sector, such as buyers, can be both a driving force and a barrier to SPPA adoption. Similarly, researchers and governments occasionally oversimplify farmers' behavior, leading to undesirable outcomes. This is likely a widespread issue stemming from limited research on the topic, communication gaps, and potential biases among researchers and extension workers.

Based on current knowledge, several solutions have been proposed. Policies or strategies that reduce risk, enhance farmers' literacy and education, and improve the accessibility of SPPAs are widely recognized as critical for promoting adoption. An emerging theme is the importance of farmer-to-farmer communication in achieving education and disseminating information effectively. These collaborative efforts, combined with targeted policies, can greatly enhance the adoption of sustainable practices.

The lack of extension services significantly hinders the adoption of SPPAs. To promote safer and more sustainable practices, improved education and policy reforms are essential (Ngowi *et al.* 2007). Researchers and policymakers must also recognize the complexity of the issue, avoiding oversimplification or quick labeling of farmers' intentions and behaviors. A more nuanced approach, involving enhanced access to training, education, and inclusion in policy development, along with a communication framework rooted in social networks rather than solely governmental channels, can address the shortcomings of existing policies (Brown *et al.* 2021).

As recent studies highlight, improving accessibility is a key factor in facilitating behavior change toward environmentally sustainable

practices (Albarracín *et al.* 2024). Creating systems that enhance the accessibility of SPPAs is crucial. Beyond financial support measures such as government subsidies, one promising solution is outsourcing SPPA-related services to extension workers, including plant doctors. This approach could reduce knowledge barriers, make SPPAs more accessible, build trust between professionals and farmers, and simultaneously create career opportunities in plant protection disciplines.

While considerable knowledge has been accumulated on factors influencing farmers' behavior and adopting SPPAs, significant gaps remain, particularly in regional studies.

Take Taiwan, for example. The government has implemented various policies to promote the adoption of SPPAs and reduce associated risks and economic burdens. The Ministry of Agriculture (MOA) and its affiliated Animal and Plant Health Inspection Agency (APHIA) have introduced several initiatives to support farmers. Since 2011, the MOA has established the "Farmers' Academy," creating a comprehensive agricultural training system to enhance farmers' knowledge and technical capacity. In 2015, the government introduced crop disaster insurance to mitigate financial risks for farmers affected by natural disasters. Additionally, the "Ten-Year Action Plan for Halving Chemical Pesticide Risks" was launched to reduce reliance on chemical pesticides and promote SPPAs. APHIA has also played an active role in encouraging sustainable practices. The agency organizes the IPM Award, recognizing individuals across the agricultural supply chain who have made outstanding contributions to IPM. Furthermore, financial incentives, such as subsidies for environmentally friendly plant protection materials- including subsidies for natural enemies used in biological control- have been implemented to facilitate the SPPAs' adoption. Despite these policies, their effectiveness remains largely unevaluated. Limited empirical evidence exists on their impact on farmers' decision-making, economic viability, and pesticide reduction, necessitating further investigation to refine and optimize policy interventions.

Agricultural systems are diverse and shaped not only by environmental factors but also by local cultures. Conducting region-specific studies is essential to account for the heterogeneity in agro-climatic and agronomic conditions that influence SPPA adoption. Such research can identify region-specific opportunities and challenges, enabling the design of tailored policies that make SPPA adoption more feasible in certain areas while addressing barriers in others. This localized approach will not only enhance SPPA promotion at regional levels but also contribute to more effective global adoption strategies. Another major gap lies in incorporating psychological perspectives into studies of farmers' behavior. Recent research has demonstrated the value of psychology in understanding factors that drive behavior change (Albarracín *et al.* 2024). Future work on SPPA adoption should integrate psychological frameworks and consider cultural and regional contexts. This approach will lead to a deeper understanding of farmer behavior and more effective strategies for promoting SPPAs.

ACKNOWLEDGMENTS

This project is supported by the National Science and Technology Council of Taiwan (Funding ID: 113-2313-B-002-044-MY3, 113WFA0111746), Yushan Fellow Program by the Ministry of Education (MOE) NTU-113V1033-2, Ministry of Agriculture of Taiwan (Funding ID: 113AS-1.3.2-AS-26).

REFERENCES

Abdollahzadeh, G., M. S. Sharifzadeh, and C. A. Damalas. 2015. Perceptions of the beneficial and harmful effects of pesticides among Iranian rice farmers influence the adoption of biological control. Crop Prot. 75:124–131. doi:10.1016/j.cropro.2015.05.018

Achabou, M. A., S. Dekhili, and M. Hamdoun. 2017. Environmental upgrading of developing country firms in global value chains. Bus. Strateg. Environ.

26:224–238. doi:10.1002/bse.1911

Agussabti, A., R. Romano, R. Rahmaddiansyah, and R. M. Isa. 2020. Factors affecting risk tolerance among small-scale seasonal commodity farmers and strategies for its improvement. Heliyon 6:e05847. doi:10.1016/j.heliyon.2020.e05847

Akter, M., L. Fan, M. M. Rahman, V. Geissen, and C. J. Ritsema. 2018. Vegetable farmers' behaviour and knowledge related to pesticide use and related health problems: A case study from Bangladesh. J. Clean. Prod. 200:122–133. doi:10.1016/j.jclepro.2018.07.130

Albarracín, D., B. Fayaz-Farkhad, and J. A. Granados Samayoa. 2024. Determinants of behaviour and their efficacy as targets of behavioural change interventions. Nat. Rev. Psychol. 3:377–392. doi:10.1038/s44159-024-00305-0

Ataei, P., S. Gholamrezai, R. Movahedi, and V. Aliabadi. 2021. An analysis of farmers' intention to use green pesticides: The application of the extended theory of planned behavior and health belief model. J. Rural Stud. 81:374–384. doi:10.1016/j.jrurstud.2020.11.003

Atreya, K. 2007. Pesticide use knowledge and practices: A gender differences in Nepal. Environ. Res. 104:305–311. doi:10.1016/j.envres.2007.01.001

Austin, E. J., I. J. Deary, and J. Willock. 2001. Personality and intelligence as predictors of economic behaviour in Scottish farmers. Eur. J. Pers. 15:S123–S137. doi:10.1002/per.421

Baker, B. P., T. A. Green, and A. J. Loker. 2020. Biological control and integrated pest management in organic and conventional systems. Biol. Control 140:104095. doi:10.1016/j.biocontrol.2019.104095

Barghusen, R., C. Sattler, L. Deijl, C. Weebers, and B. Matzdorf. 2021. Motivations of farmers to participate in collective agri-environmental schemes: The case of Dutch agricultural collectives. Ecosyst. People 17:539–555. doi:10.1080/26395916.2021.1979098

Bartkowski, B. and S. Bartke. 2018. Leverage points for governing agricultural soils: A review of empirical studies of European farmers' decision-making. Sustainability 10:3179. doi:10.3390/su10093179

Barzman, M., P. Bàrberi, A. N. E. Birch, P. Boonekamp, S. Dachbrodt-Saaydeh, B. Graf, ... M. Sattin. 2015. Eight principles of integrated pest management. Agron. Sustain. Dev. 35:1199–1215. doi:10.1007/s13593-015-0327-9

Baur, P. 2022. When farmers are pulled in too many directions: Comparing institutional drivers of food safety and environmental sustainability in California agriculture. p.241–260. *in*: Social Innovation and Sustainability Transition. (Desa, G. and X. Jia, eds.) Springer Nature, Cham, Switzerland. 390 pp. doi:10.1007/978-3-031-18560-1_17

Begho, T. 2021. Using farmers' risk tolerance to explain variations in adoption of improved rice varieties in Nepal. J. South Asian Dev. 16:171–193. doi:10.1177/09731741211023636

Bell, A., W. Zhang, and K. Nou. 2016. Pesticide use and cooperative management of natural enemy habitat in a framed field experiment. Agric. Syst. 143:1–13. doi:10.1016/j.agsy.2015.11.012

Béné, C., P. Oosterveer, L. Lamotte, I. D. Brouwer, S. de Haan, S. D. Prager, ... C. K. Khoury. 2019. When food systems meet sustainability- Current narratives and implications for actions. World Dev. 113:116–130. doi:10.1016/j.worlddev.2018.08.011

Benitez-Altuna, F., V. C. Materia, J. Bijman, D. Gaitán-Cremaschi, and J. Trienekens. 2023. Farmer–buyer relationships and sustainable agricultural practices in the food supply chain: The case of vegetables in Chile. Agribusiness 40:3–30. doi:10.1002/agr.21829

Bergner, R. M. 2020. What is personality? Two myths and a definition. New Ideas Psychol. 57:100759. doi:10.1016/j.newideapsych.2019.100759

Bhandari, H. and K. Yasunobu. 2009. What is social capital? A comprehensive review of the concept. Asian J. Soc. Sci. 37:480–510. doi:10.1163/156853109X436847

Breetz, H. L., K. Fisher-Vanden, H. Jacobs, and C. Schary. 2005. Trust and communication: Mechanisms for increasing farmers' participation in water quality trading. Land Econ. 81:170–190. doi:10.3368/le.81.2.170

Brinks, H. and S. de Kool. 2006. Farming with future: Implementation of sustainable agriculture through a network of stakeholders. p.299–303. *in*: Changing European Farming Systems for a Better Future. (Langeveld, H. and N. Röling, eds.) Wageningen Academic. 479 pp. doi:10.3920/9789086865727_076

Brown, C., E. Kovács, I. Herzon, S. Villamayor-Tomas, A. Albizua, A. Galanaki, ... Y. Zinngrebe. 2021. Simplistic understandings of farmer motivations could undermine the environmental potential of the common agricultural policy. Land Use Policy101:105136. doi:10.1016/j.landusepol.2020.105136

Chabé-Ferret, S., P. Le Coent, A. Reynaud, J. Subervie, and D. Lepercq. 2019. Can we nudge farmers into saving water? Evidence from a randomised experiment. Eur. Rev. Agric. Econ. 46:393–416. doi:10.1093/erae/jbz022

Chen, R. T., T. A. Wen, H. T. Chang, P. Lee, and M. R. Su. 2018. The certification system of Green Conservation Program. p.71–84. *in*: Proceedings of the Symposium on Organic and Eco-friendly Farming. September 14, 2018. Taichung, Taiwan. Taichung Dist. Agric. Res. Ext. Sta. No. 135. Taichung, Taiwan. (in Chinese with English abstract)

Chowdhury, A., K. H. Kabir, A. R. Abdulai, and M. F. Alam. 2023. Systematic review of misinformation in social and online media for the development of an analytical framework for agri-food sector. Sustainability 15:4753. doi:10.3390/su15064753

Codron, J. M., H. Adanacioğlu, M. Aubert, Z. Bouhsina, A. Ait El Mekki, S. Rousset, … M. Yercan. 2014. The role of market forces and food safety institutions in the adoption of sustainable farming practices: The case of the fresh tomato export sector in Morocco and Turkey. Food Policy 49:268–280. doi:10.1016/j.foodpol.2014.09.006

Costa, P. T., Jr., and R. R. McCrae. 1992. Four ways five factors are basic. Pers. Individ. Differ. 13:653–665. doi:10.1016/0191-8869(92)90236-i

Crase, L. and D. Maybery. 2004. Personality and landholders' management of remnant bush and revegetation in the Murray Catchment. Australas. J. Environ. Manag. 11:21–33. doi:10.1080/14486563.2004.10648595

Damalas, C. A. and I. G. Eleftherohorinos. 2011. Pesticide exposure, safety issues, and risk assessment indicators. Int. J. Environ. Res. Public Health 8:1402–1419. doi:10.3390/ijerph8051402

David, P., C. Roemer, R. Anibaldi, and S. Rundle-Thiele. 2022. Factors enabling and preventing farming practice change: An evidence review. J. Environ. Manage. 322:115789. doi:10.1016/j.jenvman.2022.115789

Deguine, J. P., J. N. Aubertot, S. Bellon, F. Côte, P. E. Lauri, F. Lescourret, … J. R. Lamichhane. 2023. Chapter One- Agroecological crop protection for sustainable agriculture. p.1–59. *in*: Advances in Agronomy. (Sparks, D. L., ed.) Vol. 178. Academic Press. New York, NY. 298 pp.

Deguine, J. P., J. N. Aubertot, R. J. Flor, F. Lescourret, K. A. G. Wyckhuys, and A. Ratnadass. 2021. Integrated pest management: Good intentions, hard realities. A review. Agron. Sustain. Dev. 41:38. doi:10.1007/s13593-021-00689-w

de Krom, M. P. 2017. Farmer participation in agri-environmental schemes: Regionalisation and the role of bridging social capital. Land Use Policy 60:352–361. doi:10.1016/j.landusepol.2016.10.026

Dessart, F. J., J. Barreiro-Hurlé, and R. van Bavel. 2019. Behavioural factors affecting the adoption of sustainable farming practices: A policy-oriented review. Eur. Rev. Agric. Econ. 46:417–471. doi:10.1093/erae/jbz019

Diez, J. M., C. M. D'Antonio, J. S. Dukes, E. D. Grosholz, J. D. Olden, C. J. Sorte, ... L. P. Miller. 2012. Will extreme climatic events facilitate biological invasions? Front. Ecol. Environ. 10:249–257. doi:10.1890/110137

Dubbert, C., A. Abdulai, and S. Mohammed. 2021. Contract farming and the adoption of sustainable farm practices: Empirical evidence from cashew farmers in Ghana. Appl. Econ. Perspect. Policy 45:487–509. doi:10.1002/aepp.13212

Duong, T. T., T. Brewer, J. Luck, and K. Zander. 2019. A global review of farmers' perceptions of agricultural risks and risk management strategies. Agriculture-Basel 9:10. doi:10.3390/agriculture9010010

Dyck, B. and B. S. Silvestre. 2019. A novel NGO approach to facilitate the adoption of sustainable innovations in low-income countries: Lessons from small-scale farms in Nicaragua. Organ. Stud. 40:443–461. doi:10.1177/0170840617747921

Epstein, L. and S. Bassein. 2003. Patterns of pesticide use in California and the implications for strategies for reduction of pesticides. Annu. Rev. Phytopathol. 41:351–375. doi:10.1146/annurev.phyto.41.052002.095612

Epstein, L. and M. Zhang. 2018. The impact of integrated pest management and regulation on agricultural pesticide use in California. p.203–224. *in*: Managing and Analyzing Pesticide Use Data for Pest Management, Environmental Monitoring, Public Health, and Public Policy. ACS Symposium Series. No. 1283. (Zhang, M., S. Jackson, M. A. Robertson, and M. R. Zeiss, eds.) American Chemical Society. Washington, DC. 576 pp.

Evenson, R. E. and D. Gollin. 2003. Assessing the impact of the green revolution, 1960 to 2000. Science 300:758–762. doi:10.1126/science.1078710

Finger, R. and N. Möhring. 2022. The adoption of pesticide-free wheat production and farmers' perceptions of its environmental and health effects. Ecol. Econ. 198:107463. doi:10.1016/j.ecolecon.2022.107463

Finger, R., J. Sok, E. Ahovi, S. Akter, J. Bremmer, S. Dachbrodt-Saaydeh, ... N. Möhring. 2024. Towards sustainable crop protection in agriculture: A framework for research and policy. Agric. Syst. 219:104037. doi:10.1016/j.agsy.2024.104037

Gardebroek, C. 2006. Comparing risk attitudes of organic and non-organic farmers with a Bayesian random coefficient model. Eur. Rev. Agric. Econ. 33:485–510. doi:10.1093/erae/jbl029

Grabosky, P. N. 1994. Green markets: Environmental

regulation by the private sector. Law Policy 16:419–448. doi:10.1111/j.1467-9930.1994.tb00132.x

Grimm, P. 2010. Social desirability bias. *in*: Wiley International Encyclopedia of Marketing (Sheth, J. and N. Malhotra, eds.). John Wiley & Sons. Hoboken, NJ. 1760 pp. doi:10.1002/9781444316568.wiem02057

Guo, L., H. Li, X. Cao, A. Cao, and M. Huang. 2021. Effect of agricultural subsidies on the use of chemical fertilizer. J. Environ. Manage 299:113621. doi:10.1016/j.jenvman.2021.113621

He, J., W. Zhou, S. Guo, X. Deng, J. Song, and D. Xu. 2023. Environmental policy and farmers' active straw return: Administrative guidance or economic reward and punishment. Environ. Dev. Sustain. 26:17407–17430. doi:10.1007/s10668-023-03345-3

Hoque, M. N., S. M. Saha, S. Imran, A. Hannan, M. M. H. Seen, S. S. Thamid, and F. Tuz-zohra. 2022. Farmers' agrochemicals usage and willingness to adopt organic inputs: Watermelon farming in Bangladesh. Environ. Chall. 7:100451. doi:10.1016/j.envc.2022.100451

Horrigan, L., R. S. Lawrence, and P. Walker. 2002. How sustainable agriculture can address the environmental and human health harms of industrial agriculture. Environ. Health Perspect. 110:445–456. doi:10.1289/ehp.02110445

Huang, C. L., C. Y. Lin, L. C. Li, C. J. Lai, and P. C. Chung. 2022. Establishment of farmer's operational evaluation criteria in the early stage of IPM introduction- Taking Miaoli strawberry farmers as an example. p.15–36. *in*: MDARES Bulletin. (Lu, M. C., ed.) Miaoli Dist. Agric. Res. Ext. Sta. No. 11. Miaoli, Taiwan. (in Chinese with English abstract)

Ilbery, B. and I. Bowler. 2014. From agricultural productivism to post-productivism. p.57–84. *in*: The Geography of Rural Change. (Ilbery, B., ed.) Routledge. New York, NY. 280 pp.

Intergovernmental Panel on Climate Change (IPCC). 2021. Climate Change 2021: The Physical Science Basis. https://www.ipcc.ch/report/ar6/wg1 (visit on 1/15/2025)

International Plant Protection Convention (IPPC). 2021. Scientific Review of the Impact of Climate Change on Plant Pests- A Global Challenge to Prevent and Mitigate Plant Pest Risks in Agriculture, Forestry and Ecosystems. FAO on behalf of the IPPC Secretariat. Rome, Italy. 72 pp. doi:10.4060/cb4769en

Jin, S., B. Bluemling, and A. P. J. Mol. 2015. Information, trust and pesticide overuse: Interactions between retailers and cotton farmers in China. NJAS Wageningen J. Life Sci. 72–73:23–32. doi:10.1016/j.njas.2014.10.003

Klonsky, K. 2012. Comparison of production costs and resource use for organic and conventional production systems. Am. J. Agric. Econ. 94:314–321. doi:10.1093/ajae/aar102

Knapp, L., D. Wuepper, and R. Finger. 2021. Preferences, personality, aspirations, and farmer behavior. Agric. Econ. 52:901–913. doi:10.1111/agec.12669

Kouame, R. M. A., F. Guglielmo, K. Abo, A. F. Ouattara, J. Chabi, L. Sedda, … C. Edi. 2022. Education and socio-economic status are key factors influencing use of insecticides and malaria knowledge in rural farmers in Southern Cote d'Ivoire. BMC Public Health 22:2443. doi:10.1186/s12889-022-14446-5

Kuhfuss, L., R. Préget, S. Thoyer, and N. Hanley. 2016. Nudging farmers to enrol land into agri-environmental schemes: The role of a collective bonus. Eur. Rev. Agric. Econ. 43:609–636. doi:10.1093/erae/jbv031

Latawiec, A. E., B. B. N. Strassburg, D. Silva, H. N. Alves-Pinto, R. Feltran-Barbieri, A. Castro, … F. Beduschi. 2017. Improving land management in Brazil: A perspective from producers. Agric. Ecosyst. Environ. 240:276–286. doi:10.1016/j.agee.2017.01.043

Li, H., J. Liu, and W. Y. Chang. 2024. Influence of self-identity and social identity on farmers' willingness for cultivated land quality protection. Land 13:1392. doi:10.3390/land13091392

Li, H., C. Wang, W. Y. Chang, and H. Liu. 2023. Factors affecting Chinese farmers' environment-friendly pesticide application behavior: A meta-analysis. J. Clean. Prod. 409:137277. doi:10.1016/j.jclepro.2023.137277

Li, H., K. Yuan, A. Cao, X. Zhao, and L. Guo. 2022. The role of crop insurance in reducing pesticide use: Evidence from rice farmers in China. J. Environ. Manage. 306:114456. doi:10.1016/j.jenvman.2022.114456

Lo, W. F. 2024. Embracing plural values of nature in eco-friendly Participatory Guarantee System: A case study of Green Conservation label. Master Thesis. Department of Agricultural Economics, National Taiwan University. Taipei, Taiwan. 120 pp. (in Chinese with English abstract)

Lundgren, J. G. and S. W. Fausti. 2015. Trading biodiversity for pest problems. Sci. Adv. 1:e1500558. doi:10.1126/sciadv.1500558

Lykogianni, M., E. Bempelou, F. Karamaouna, and K. A. Aliferis. 2021. Do pesticides promote or hinder sustainability in agriculture? The challenge of sustainable use of pesticides in modern agriculture. Sci. Total Environ. 795:148625. doi:10.1016/j.scitotenv.2021.148625

Martin, S., A. Rieple, J. Chang, B. Boniface, and A.

Ahmed. 2015. Small farmers and sustainability: Institutional barriers to investment and innovation in the Malaysian palm oil industry in Sabah. J. Rural Stud. 40:46–58. doi:10.1016/j.jrurstud.2015.06.002

Martins, C. M., S. C. F. Pereira, M. R. S. Scarpin, M. M. Queiroz, and M. D. S. Cavalcante. 2025. The impact of customer pressures and government regulations on the implementation of socio-environmental practices in organic certification in the Amazon region. Benchmarking 32:1099–1119. doi:10.1108/bij-07-2023-0453

Matthews, G. A. 2018. A History of Pesticides. Centre for Agriculture and Biosciences International. Wallingford, Oxfordshire, UK. 288 pp.

Mattson, W. J. and R. A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. BioScience 37:110–118. doi:10.2307/1310365

McGovern, R. J. and C. To-Anun. 2016. Plant doctors: A critical need. Int. J. Agric. Technol. 12:1175–1193

Meunier, E., P. Smith, T. Griessinger, and C. Robert. 2024. Understanding changes in reducing pesticide use by farmers: Contribution of the behavioural sciences. Agric. Syst. 214:103818. doi:10.1016/j.agsy.2023.103818

Michel-Guillou, E. and G. Moser. 2006. Commitment of farmers to environmental protection: From social pressure to environmental conscience. J. Environ. Psychol. 26:227–235. doi:10.1016/j.jenvp.2006.07.004

Mills, J., P. Gaskell, J. Ingram, J. Dwyer, M. Reed, and C. Short. 2017. Engaging farmers in environmental management through a better understanding of behaviour. Agric. Hum. Values 34:283–299. doi:10.1007/s10460-016-9705-4

Mkenda, P., R. Mwanauta, P. C. Stevenson, P. Ndakidemi, K. Mtei, and S. R. Belmain. 2015. Extracts from field margin weeds provide economically viable and environmentally benign pest control compared to synthetic pesticides. PLOS ONE 10:e0143530. doi:10.1371/journal.pone.0143530

Möhring, N., T. Dalhaus, G. Enjolras, and R. Finger. 2020. Crop insurance and pesticide use in European agriculture. Agric. Syst. 184:102902. doi:10.1016/j.agsy.2020.102902

Nastis, S. A., K. Mattas, and G. Baourakis. 2019. Understanding farmers' behavior towards sustainable practices and their perceptions of risk. Sustainability 11:1303. doi:10.3390/su11051303

Ngowi, A. V., T. J. Mbise, A. S. Ijani, L. London, and O. C. Ajayi. 2007. Pesticides use by smallholder farmers in vegetable production in Northern Tanzania. Crop Prot. 26:1617–1624. doi:10.1016/j.cropro.2007.01.008

Oerlemans, N. and G. Assouline. 2004. Enhancing farmers' networking strategies for sustainable development. J. Clean. Prod. 12:469–478. doi:10.1016/S0959-6526(03)00105-7

Peeters, F., J. van Meggelen, and H. T. A. M. Schepers 2015. Crop protection and pesticide risk assessment Myanmar: Towards sustainable agricultural and export of high value crops. Alterra. Wageningen, Netherland. 81 pp.

Peng, W., N. L. Ma, D. Zhang, Q. Zhou, X. Yue, S. C. Khoo, ... C. Sonne. 2020. A review of historical and recent locust outbreaks: Links to global warming, food security and mitigation strategies. Environ. Res. 191:110046. doi:10.1016/j.envres.2020.110046

Phung, Q. A. and N. Dao. 2024. Farmers' perceptions of sustainable agriculture in the Red River Delta, Vietnam. Heliyon 10:e28576. doi:10.1016/j.heliyon.2024.e28576

Pierrette Coulibaly, T., J. Du, D. Diakité, O. J. Abban, and E. Kouakou. 2021. A proposed conceptual framework on the adoption of sustainable agricultural practices: The role of network contact frequency and institutional trust. Sustainability 13:2206. doi:10.3390/su13042206

Pirmoradi, A. and F. Rostami. 2021. Farmers' unsustainable behavior: Application of the integrative agent-centered (IAC) framework. Environ. Dev. Sustain. 24:13542–13556. doi:10.1007/s10668-021-01999-5

Qiao, D., S. Xu, T. Xu, Q. Hao, and Z. Zhong. 2022. Gap between willingness and behaviors: Understanding the consistency of farmers' green production in Hainan, China. Int. J. Environ. Res. Public Health 19:11351. doi:10.3390/ijerph191811351

Ren, C., S. Liu, H. van Grinsven, S. Reis, S. Jin, H. Liu, and B. Gu. 2019. The impact of farm size on agricultural sustainability. J. Clean. Prod. 220:357–367. doi:10.1016/j.jclepro.2019.02.151

Ren, Z., Z. Fu, and K. Zhong. 2022. The influence of social capital on farmers' green control technology adoption behavior. Front. Psychol. 13:1001442. doi:10.3389/fpsyg.2022.1001442

Risch, S. J. 1987. Agricultural ecology and insect outbreaks. p.217–238. *in*: Insect Outbreaks. (Barbosa, P. and J. C. Schultz, eds.) Academic Press. San Diego, CA. 578 pp.

Rogers, S., Z. J. H. Wang, and J. He. 2023. Farmers' practices and the political ecology of agrochemicals in rural China. Geoforum 141:103751. doi:10.1016/j.geoforum.2023.103751

Rust, N. A., P. Stankovics, R. M. Jarvis, Z. Morris-Trainor, J. R. de Vries, J. Ingram, ... M. S. Reed. 2022. Have

farmers had enough of experts? Environ. Manage. 69:31–44. doi:10.1007/s00267-021-01546-y

Sánchez-Bayo, F. 2021. Indirect effect of pesticides on insects and other arthropods. Toxics 9:177. doi:10.3390/toxics9080177

Savary, S., L. Willocquet, S. J. Pethybridge, P. Esker, N. McRoberts, and A. Nelson. 2019. The global burden of pathogens and pests on major food crops. Nat. Ecol. Evol. 3:430–439. doi:10.1038/s41559-018-0793-y

Scherfranz, V., K. Moon, J. Kantelhardt, A. Adler, S. Barreiro, F. V. Bodea, ... L. Schaller. 2024. Using a perception matrix to elicit farmers' perceptions towards stakeholders in the context of biodiversity-friendly farming. J. Rural Stud. 108:103282. doi:10.1016/j.jrurstud.2024.103282

Schneider, L., M. Rebetez, and S. Rasmann. 2022. The effect of climate change on invasive crop pests across biomes. Curr. Opin. Insect Sci. 50:100895. doi:10.1016/j.cois.2022.100895

Shahidullah, A. K. M., A. Islam, and M. Rahman. 2023. Knowledge, attitude, and practice of pesticide use by vegetable growers in Bangladesh: A health literacy perspective in relation to non-communicable diseases. Front. Sustain. Food Syst. 7:1199871. doi:10.3389/fsufs.2023.1199871

Sharifzadeh, M. S., G. Abdollahzadeh, C. A. Damalas, and R. Rezaei. 2018. Farmers' criteria for pesticide selection and use in the pest control process. Agriculture-Basel 8:24. doi:10.3390/agriculture8020024

Shen, L. and F. Wang. 2024. Can market-oriented allocation of land factors promote the adoption of cropland quality protection behaviors by farmers: Evidence from rural China. Land 13:665. doi:10.3390/land13050665

Stavins, R. N. 1989. Harnessing market forces to protect the environment. Environment 31:5–35. doi:10.1080/00139157.1989.9929926

Sulemana, I. and H. S. James Jr. 2014. Farmer identity, ethical attitudes and environmental practices. Ecol. Econ. 98:49–61. doi:10.1016/j.ecolecon.2013.12.011

Sutherland, L. A., J. Mills, J. Ingram, R. J. F. Burton, J. Dwyer, and K. Blackstock. 2013. Considering the source: Commercialisation and trust in agri-environmental information and advisory services in England. J. Environ. Manage. 118:96–105. doi:10.1016/j.jenvman.2012.12.020

Teng, Y., B. Pang, J. Wei, L. Ma, H. Yang, and Z. Tian. 2022. Behavioral decision-making of the government, farmer-specialized cooperatives, and farmers regarding the quality and safety of agricultural products. Front. Public Health 10:920936. doi:10.3389/fpubh.2022.920936

Thuerig, B. and L. Tamm. 2020. Development of plant-derived compounds as biopesticides. p.315–334. *in*: Biopesticides for Sustainable Agriculture. (Birch, N. and T. Glare, eds) Burleigh Dodds Science Publishing. Cambridge, UK. 366 pp.

Tilman, D., C. Balzer, J. Hill, and B. L. Befort. 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U.S.A. 108:20260–20264. doi:10.1073/pnas.1116437108

Toma, L. and E. Mathijs. 2007. Environmental risk perception, environmental concern and propensity to participate in organic farming programmes. J. Environ. Manage. 83:145–157. doi:10.1016/j.jenvman.2006.02.004

Tomar, P., N. Thakur, S. Jhamta, S. Chowdhury, M. Kapoor, S. Singh, … A. N. Yadav. 2024. Bacterial biopesticides: Biodiversity, role in pest management and beneficial impact on agricultural and environmental sustainability. Heliyon 10:e31550. doi:10.1016/j.heliyon.2024.e31550

Tucker, M. and T. L. Napier. 2001. Determinants of perceived agricultural chemical risk in three watersheds in the Midwestern United States. J. Rural Stud. 17:219–233. doi:10.1016/S0743-0167(00)00044-9

Van der Ploeg, J. D., C. Laurent, F. Blondeau, and P. Bonnafous. 2009. Farm diversity, classification schemes and multifunctionality. J. Environ. Manage. 90:S124–S131.

Villamayor-Tomas, S., J. Sagebiel, and R. Olschewski. 2019. Bringing the neighbors in: A choice experiment on the influence of coordination and social norms on farmers' willingness to accept agro-environmental schemes across Europe. Land Use Policy 84:200–215. doi:10.1016/j.landusepol.2019.03.006

Wan, M., R. Gu, T. Zhang, Y. Zhang, H. Ji, B. Wang, … S. Toepfer. 2019. Conflicts of interests when connecting agricultural advisory services with agri-input businesses. Agriculture-Basel 9:218. doi:10.3390/agriculture9100218

Wang, X., X. Cui, and X. Sun. 2024. How to promote the application of green pesticides by farmers? Evolutionary game analysis based on "government–farmer–consumer". Front. Environ. Sci. 12:1326709. doi:10.3389/fenvs.2024.1326709

Wezel, A., M. Casagrande, F. Celette, J. F. Vian, A. Ferrer, and J. Peigne. 2014. Agroecological practices for sustainable agriculture. A review. Agron. Sustain. Dev. 34:1–20. doi:10.1007/s13593-013-0180-7

Wilson, G. A. and K. Hart. 2000. Financial imperative or conservation concern? EU farmers' motivations for participation in voluntary agri-environmen-

tal schemes. Environ. Plan. A. 32:2161–2185. doi:10.1068/a3311

Wuepper, D., N. Roleff, and R. Finger. 2021. Does it matter who advises farmers? Pest management choices with public and private extension. Food Policy 99:101995. doi:10.1016/j.foodpol.2020.101995

Wyckhuys, K. A. G. and R. J. O. Neil. 2007. Local agro-ecological knowledge and its relationship to farmers' pest management decision making in rural Honduras. Agric. Hum. Values. 24:307–321. doi:10.1007/s10460-007-9068-y

Xiang, W. and J. Gao. 2023. Do not be anticlimactic: Farmers' behavior in the sustainable application of green agricultural technology- A perceived value and government support perspective. Agriculture 13:247. doi:10.3390/agriculture13020247

Xu, X., F. Wang, T. Xu, and S. U. Khan. 2023. How does capital endowment impact farmers' green production behavior? Perspectives on ecological cognition and environmental regulation. Land 12:1611. doi:10.3390/land12081611

Yang, Y., Y. Yu, R. Li, and D. Jiang. 2023. Impact of pesticide outsourcing services on farmers' low-carbon production behavior. Front. Environ. Sci. 11:1226039. doi:10.3389/fenvs.2023.1226039

Yen, A. and Y. Che. 2021. The key role of leadership in promoting environmentally friendly farming- The case of Wufeng District in Taichung. J. Taiwan Land Res. 24:101–137. (in Chinese with English abstract) doi:10.6677/JTLR.202111_24(2).0001

Yoshida, Y., C. G. Flint, and M. K. Dolan. 2018. Farming between love and money: US Midwestern farmers' human-nature relationships and impacts on watershed conservation. J. Environ. Plan. Manag. 61:1033–1050. doi:10.1080/09640568.2017.1327423

Zaccone, M. C. and M. Pedrini. 2020. ESG factor integration into private equity. Sustainability 12:5725. doi:10.3390/su12145725

Zhang, S. and X. Zhang. 2024. Fiscal agricultural expenditures' impact on sustainable agricultural economic development: Dynamic marginal effects and impact mechanism. PLOS ONE 19:e0299070. doi:10.1371/journal.pone.0299070

Zheng, S., K. Yin, and L. Yu. 2022. Factors influencing the farmer's chemical fertilizer reduction behavior from the perspective of farmer differentiation. Heliyon 8:e11918. doi:10.1016/j.heliyon.2022.e11918

Zhou, X. and M. Han. 2024. Tripartite evolutionary game analysis of government reward and punishment mechanisms and agricultural resilience under a dual carbon context. China Agric. Econ. Rev. 17:64–88. doi:10.1108/caer-01-2024-0018

農民採用永續植物保護措施的誘因

林柏安 [1,*]　廖婉頤 [2]　何率慈 [3]　謝佳維 [4]　李宗翰 [5]

摘要

林柏安、廖婉頤、何率慈、謝佳維、李宗翰。2025。農民採用永續植物保護措施的誘因。台灣農業研究 74(2):87–112。

永續植物保護措施 (sustainable plant protection approaches; SPPAs) 在減輕有害生物防治所引發的環境衝擊與促進永續農業系統的建立方面，具有關鍵重要性。本專題論述統整影響農民採用 SPPAs 的多重因素，並著重於不同層級因素與其交互作用。與農戶相關 (farm-related) 的因素包括健康風險、風險認知、經濟能力以及對 SPPAs 成效與實施方式的理解；而非農戶層面的因素 (non-farm-related) 則涵蓋社會規範、政府政策以及與利害關係人的互動，這些因素同樣影響 SPPAs 的採用行為。現有研究顯示，社會網絡 (如農民間的互動) 與推廣服務，在知識傳遞與 SPPAs 採用過程中扮演關鍵機制。儘管 SPPAs 在環境與經濟層面有顯著益處，但高成本、成效認知不足以及有限的資訊與技術資源，仍為農民採用 SPPAs 的主要障礙。政府介入，如提供補助、培訓計畫及作物保險，為降低 SPPAs 相關風險與經濟負擔的重要工具。但政策碎片化與市場壓力的矛盾，往往對 SPPAs 的推廣形成阻礙。總結過去研究，若要提升 SPPAs 之採用，建立整合且基於實證的政策，協調各方利害關係人的激勵機制，並運用行為科學與心理學促進農民採用 SPPAs，同時考量區域文化差異為相當重要的工作。然而，目前相關研究相對匱乏。推動 SPPAs 的廣泛應用，仰賴長期研究與研究人員、政策制定者及農業組織的協同合作，以構建具韌性且永續的植物保護策略與農業生產體系。

關鍵詞：農民行為、整合性有害生物管理 (IPM)、農業永續、農業政策、利害關係人。

投稿日期：2025 年 2 月 20 日；接受日期：2025 年 4 月 2 日。

[*] 通訊作者：poanlin@ntu.edu.tw
[1] 國立臺灣大學昆蟲學系助理教授。臺灣 臺北市。
[2] 吉田田有限公司研究員及產品經理。臺灣 臺南市。
[3] 國立臺灣大學農業經濟學系助理教授。臺灣 臺北市。
[4] 國立臺灣大學昆蟲學系大學生。臺灣 臺北市。
[5] 農業部農業藥物試驗所農藥應用組助理研究員。臺灣 臺中市。

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):113–128 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0002

Feature Article

Advancing Invasive Ant Management: Innovative and Targeted Strategies

Fang-Ling Chloe Liu[1], Shu-Ping Tseng[2], Chung-Chi Lin[3], and Chin-Cheng Scotty Yang[4,*]

Abstract

Liu, F. L. C., S. P. Tseng, C. C. Lin, and C. C. S. Yang. 2025. Advancing invasive ant management: Innovative and targeted strategies. J. Taiwan Agric. Res. 74(2):113–128.

Invasive ant management has evolved from relying solely on broad-spectrum toxic baits to incorporating more targeted, environmentally friendly strategies. This shift toward precision and sustainability inspires future management to focus on integrated, species-specific, and cost-effective approaches. This review highlights innovative approaches, including hydrogel bait formulations, foraging disruption/enhancement via species-specific trail pheromones, insecticide-coated prey baits, and microbial control agents to enhance effectiveness. We also highlighted several advanced techniques involving RNA interference and AI-powered tools that can be integrated into the current invasive ant management framework. Throughout the review, we outline the advantages and limitations of each method under various field scenarios, offering insights into how these innovations can be effectively integrated into invasive ant management. We also emphasize the strategy of utilizing different methods to respond to varying population density levels to maximize control efficacy while minimizing non-target impacts. Tailoring management tactics to population dynamics allows for aggressive suppression during peak infestations and the use of species-specific tools to support ecosystem recovery as populations decline.

Key words: Invasive ant, Baiting, Hydrogel, Biorational control, Artificial intelligence.

INTRODUCTION

Human activities have increasingly facilitated the global spread of invasive species, resulting in significant economic and ecological consequences worldwide (Bertelsmeier *et al.* 2017; Sardain *et al.* 2019). In 2019, the annual global cost of biological invasions was estimated to exceed US$423 billion (Diagne *et al.* 2021; Roy *et al.* 2023). Among invasive alien species, ants are one of the most damaging taxa, with an estimated annual economic impact of US$119 million (Angulo *et al.* 2022). While invasive ants are typically not problematic in their native ecosystems, they can become highly disruptive pests in introduced regions, causing ecological and economic harm (Holway *et al.* 2002). Well-known invasive ant species including the red imported fire ant (*Solenopsis invicta*), Argentine ant (*Linepithema humile*), little fire ant (*Wasmannia auropunctata*), tawny crazy ant (*Nylanderia fulva*), yellow crazy ant (*Anoplolepis gracilipes*), Asian needle ant (*Brachyponera chinensis*), and African big-headed ant (*Pheidole megacephala*). The development of invasive ant management tools has progressed alongside advancements in technology, with

Received: January 25, 2025; Accepted: April 23, 2025.
* Corresponding author, e-mail: scottyyang@vt.edu
1 PhD Candidate, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.
2 Assistant Professor, Department of Entomology, National Taiwan University, Taipei, Taiwan.
3 Distinguished Professor, Department of Biology, National Changhua University of Education, Changhua, Taiwan.
4 Assistant Professor, Department of Entomology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA.

a growing emphasis on improving species specificity, enhancing efficacy, and ensuring cost-effectiveness. In this review, we examine the history and evolution of invasive ant management, with a particular focus on the rise of conventional baiting strategies. We then explore emerging control approaches including several biorational control innovation (defined as the use of specific and selective chemical, biological and physical agents for controlling pests which results in minimum no-target impacts; Haddi *et al.* 2020) and conclude with insights into future directions for invasive ant management.

EVOLUTION OF INVASIVE ANT CONTROL: TRANSITIONING FROM CONTACT INSECTICIDE TO BAIT

Residual insecticide treatments were initially employed to manage invasive ants with different formulations adapting to different scenarios (Klotz *et al.* 1995). Treatments incorporating repellent insecticide at perimeter inside or around human structures can knockdown foraging workers, disrupt the establishment of foraging trails, and prevent ants from entering (Knight & Rust 1990; Klotz *et al.* 2007). Instead of the rapid contact toxic effect, non-repellent insecticides can be transferred within colonies through worker contacts (e.g., grooming and necrophoresis) (Soeprono & Rust 2004; Choe & Rust 2008; Wiltz *et al.* 2010). While residual insecticide treatments result in rapid and significant reduction in foraging workers, they rarely achieve colony eradication, as reproductives (e.g., queens and winged alates) may remain unaffected (Edwards 1986; Soeprono & Rust 2004). In response to treatment, ant colonies may migrate to avoid further contact with these fast-acting insecticides, potentially leading to secondary invasions and promoting the spread of invasive ants (Buczkowski *et al.* 2005; Buczkowski 2024). Beyond such inefficiency, residual spray applications raise concerns about increased insecticide usage, which can result in runoff into urban waterways (Greenberg *et al.* 2010; Gan *et al.* 2012; Jiang *et al.* 2014) as well as increased exposure to humans, pets and other non-target organisms (Hoffmann *et al.* 2016; Sakamoto *et al.* 2019). To address these disadvantages, several alternative control strategies have been developed and evaluated, with toxic baits being the most emphasized management tool (Klotz *et al.* 1997). Toxic baits, which are insecticide-impregnated food, take advantage of ants' extensive foraging and food-sharing (i.e., trophallaxis) behaviors that facilitate bait transport into the nest and share it with nestmates (Davis & van Schagen 1993). Coupled with the delayed toxicity, the toxicant has a higher chance of reaching in-nest members including nurse workers, larvae, and even queens, leading to mortality or reduced colony reproduction (Rust *et al.* 2004). Toxic baits have since become the preferred invasive ant control method, attributed to their greater efficacy, cost-effectiveness and ease of application. The toxicants used in baits contain low doses of toxins but vary in their speed of control depending on the specific active ingredient. Taking fire ant baits as an example, Advion® fire ant bait contains 0.45% indoxacarb and results in rapid mortality within a week, while Extinguish® fire ant bait, which uses an insect growth regulator (0.5% s-methoprene) as active ingredient, takes 3–6 mo to control fire ants (Table 1).

CONVENTIONAL BAITS

An effective bait should be easy to transport and attract target ants. Consisting of attractants, carriers, sometimes additives, and active ingredients, conventional bait development focuses on testing preferences for different bait formulations (liquid, gel, granules) and the nutrient composition of food attractants (e.g., lipid, protein, and carbohydrate) to ensure the attractiveness and recruitment of target ant spe-

Table 1. Active ingredients in fire ant bait products.

Active ingredients	Mode of action	Bait trade name	Speed of control
Indoxacarb	Voltage-dependent sodium channel blockers	Advion® (0.45%)	2–7 d
Metaflumizone	Voltage-dependent sodium channel blockers	Altrevin™/Siesta™ (0.063%)	1–4 wk
Fipronil	γ-aminobutyric acid (GABA)-gated chloride channel blockers	Maxforce® FC (0.00045%)	2–6 wk
Hydramethylnon	Mitochondrial complex III electron transport inhibitors	Amdro®/Amdro Pro®/ Probait® (0.73%) Amdro® Ant Block (0.88%)	2–6 wk
Spinosad	Nicotinic acetylcholine receptor (nAChR) allosteric modulators - Site I	CONSERVE® (0.015%)	2–6 wk
Abamectin	Glutamate-gated chloride channel allosteric modulators	Ascend™/Advance™/Clinch®/Awards® II (0.011%)	2–4 mo
Pyriproxyfen	Juvenile hormone receptor modulators	Distance®/Esteem® (0.5%)	2–6 mo
s-Methoprene	Insect growth regulator	Extinguish® (0.5%)	3–6 mo
s-Methoprene + Hydramethylnon	Insect growth regulator + Mitochondrial complex III electron transport inhibitors	Extinguish® Plus (0.25% s-methoprene and 0.36% hydramethylnon) Amdro® Yard Treatment Bait (0.0172% s-methoprene and 0.036% hydramethylnon)	2–4 wk

cies. For example, sugary liquid baits attract a wide range of ants, especially those primarily feeding on liquid sugars (e.g., honeydew and nectar) such as the Argentine ant, *L. humile* (Krushelnycky & Reimer 1998; Rust *et al.* 2000). Protein- or oil-rich granular baits are most effective against the red imported fire ant, *S. invicta* and the big-headed ant, *P. megacephala* (Loke & Lee 2004; Neff *et al.* 2011). While baiting is the major strategy for controlling invasive ants, several disadvantages and limitations have been identified. First, worker ants may remain active and cause negative impacts during post-treatment period because active ingredients in baits are typically in low doses and slow-acting (Oi & Oi 2006; Klotz *et al.* 2007). Second, bait formulations are limited in use: liquid and gel baits are typically suitable for indoor use due to their relatively short lifespan under field conditions, while granular baits can be used outdoors but with reduced effectiveness after irrigation or precipitation (Klotz 2010). Advanced water-resist carriers have been proposed to overcome this disadvantage. Hydrophobic baits provide greater accessibility to foraging ants and have been evaluated and proven effective in controlling *S. invicta* and *W. auropunctata* under moist conditions (Kafle *et al.* 2010, 2015; Vander Meer & Milne 2017; Oi *et al.* 2022a, 2022b). Third, baits containing general phagostimulants may attract other non-target ant species (Zakharov & Thompson 1998). While suppressing target invasive ant species, baiting could reduce the populations of competing ants (Sakamoto *et al.* 2019). Lastly, bait acceptance may be interfered by risks perceived by foraging ants, such as the presence of toxicants or phorid flies (Orr & Seike 1998; Folgatait & Gilbert 1999; Josens *et al.* 2016; Zanola *et al.* 2024).

HYDROGEL

Hydrogels represent an innovative solution for invasive ant management, addressing the limitations of traditional liquid baits, such as fermentation, water loss, and labor-intensive maintenance (Boser *et al.* 2014). These super-absorbent bait matrices, whether synthetic or natural alginate-based, are highly attractive to invasive ants such as *L. humile* and can be deployed cost-effectively without dispensers, reducing labor and insecticide use while posing minimal risk to non-target organisms (Rust *et al.*

2015; Tay *et al.* 2017; McCalla *et al.* 2020). While *L. humile* does not always locate hydrogel baits in the field faster than other ant species in the field, they tend to occupy the hydrogels with a large number of workers and exclude other interspecific competitors (Cabrera *et al.* 2021). Despite challenges such as rapid dehydration in hot, dry conditions and incompatibility with non-water-soluble active ingredients, the hydrogel delivery system has effectively controlled several invasive ant species, including *L. humile* (Rust *et al.* 2015; Tay *et al.* 2017; McCalla *et al.* 2020; Le *et al.* 2023; Milosavljević *et al.* 2024), *N. fulva* (McCalla *et al.* 2020), *A. gracilipes* (Peck *et al.* 2017; Lee *et al.* 2025), and *Technomyrmex brunneus* (Sunamura *et al.* 2022; Terayama *et al.* 2025). Although direct efficiency comparisons between traditional bait and hydrogels are limited, Choe *et al.* (2021) demonstrated that a low-impact integrated pest management (IPM) model incorporating boric acid hydrogels is more effective at maintaining low Argentine ant densities around home perimeters than conventional spray-based treatments (Table 2). The hydrogel delivery system uses less insecticide, thereby minimizing toxicant runoff (McCalla *et al.* 2020). Additional empirical works have further demonstrated that hydrogels pose a low risk to non-target organisms, particularly pollinator insects, due to extremely low attractiveness (Buczkowski 2020; Hoffmann 2023). Several improvements have been suggested in hydrogel baits, including (1) placing the beads near irrigation point allowing them being rehydrated (Rust *et al.* 2015; Tay *et al.* 2017; Cabrera *et al.* 2021); (2) incorporating synthetic trail pheromones with hydrogel baits to increase the species-specificity (Choe *et al.* 2021); (3) adjusting the size of hydrogel beads to meet the best bait acceptance and attractiveness rate to target invasive ants (Lee *et al.* 2025); and (4) development of dry form that is easier to transport and store, to be hydrated before application (McCalla *et al.* 2020; Tay *et al.* 2020).

FORAGING DISRUPTION/ ENHANCEMENT

Ant trail pheromones, species-specific chemical compounds used for recruitment, have been studied extensively. Notable examples include (Z)-9-hexadecenal in *L. humile* (Cavill *et al.* 1979) and (Z,E)-α-farnesene in *S. invicta* (Vander Meer *et al.* 1988). Synthetic trail pheromones disrupt natural foraging by increasing turning behavior and disorientating them from natural foraging trails (Suckling *et al.* 2008, 2010, 2012; Tanaka *et al.* 2009). These trail-disrupting effects could lead to reduced foraging activity and colony food shortages, eventually resulting in population decline. However, standalone pheromone treatments show limited long-term effects (Nishisue *et al.* 2010). Greater efficacy is achieved when combined with other control methods. For example, integrating (Z)-9-hexadecenal with toxic baits or residual sprays enhances control by attracting *L. humile* to treated surfaces (Choe *et al.* 2014, 2021) or increasing bait consumption, reducing insecticide use while boosting control efficiency (Greenberg & Klotz 2000; Choe *et al.* 2014; Welzel & Choe 2016; Sunamura 2018). Similar controlling effects have been observed with pheromone-assisted liquid bait for the invasive European fire ant, *Myrmica rubra* (Hoefele *et al.* 2020). Ant pheromones not only disrupt specifically target ant species but have also been demonstrated to discriminate other non-target species, such as honey bee, reducing their contact with the toxins (Sidhu & Wilson Rankin 2016). However, the species-specific nature of pheromone-assisted technique can be a double-sword. While they effectively minimize non-target effects, their impact is limited to a single ant species. This limitation may pose challenges in areas where multiple invasive ant species coexist (Sunamura 2018).

Table 2. Comparative analysis of control methods based on insecticide reliance, cost, species specificity, and limitations.

Method	Description	Insecticide reliance	Cost (excluding labor cost)	Species specificity	Limitations
Conventional baits-granular	Solid form, distributable via dispenser, suitable for outdoor use	High	Advion: $33 per acre based on labeled application rate	Low	(1) Risk of insecticide run-off and non-target effects (2) Reduced effectiveness after precipitation (Advanced: water-resist granular baits)
Conventional baits-liquid	Liquid form, targeting sugar-loving ants, distributed by bait station, suitable for indoor and outdoor use	High	Boric acid: < $1 per home (5.6 L needed under the low-impact integrated pest management (IPM) model)[z]/$20–32 per bait station	Low	(1) Risk of insecticide run-off and non-target effects (2) Require bait station and frequent inspection and replacement, which incurs additional labor cost
Hydrogel	A controlled-release system formulated with a polymeric matrix, applicable directly without a bait station. It requires less insecticide and can be rehydrated by irrigation or precipitation	Low	$5.6 per home (5.6 L needed under the low-impact IPM model)[z]	Medium (reduced attractiveness to pollinators)	(1) Dehydration and thus reduction in attractiveness (2) Require a water-soluble active ingredient
Foraging disruption/ enhancement	Utilizes synthetic trail pheromone of the target ant species, incorporated with toxic baits/insecticide sprays to increase species specificity and reduce insecticide usage	Low	$6.16 per home (6.5 L needed under the low-impact IPM model)[z]	High	(1) Less effective when used alone (2) Limited to the target ant species only (3) Less effective for settings where multiple invasive ants co-exist
Insecticide-coated prey baits	Using live prey as an insecticide carrier enhances bait selectivity. Suitable for ant species lacking a trail pheromone system	Low	No labeled rates available but potentially high	High	(1) High labor cost (2) Need live prey
RNA interference (RNAi)	Oral delivery synthetic double-stranded RNA (dsRNA) silence target genes post-transcriptionally, highly species-specific	None	No labeled rates available but potentially high	High	Requires carriers to protect dsRNA from degradation under field conditions
Viral pathogens	Artificially inoculates a species-specific virus that causes adverse effects. The virus is sustainable in the field and can spread between colonies	None	No labeled rates available but potentially low	High	(1) Only applicable to areas where target virus is absent (2) Consider the effects of virus-induced behavioral changes on target ants

[z] Choe *et al.* (2021)

INSECTICIDE-COATED PREY BAITS

Often known as the "Trojan horse approach", prey-baiting was first proposed by Williams (1986). This method uses live prey, such as fly pupae preferred by *S. invicta*, as carriers for insecticides, facilitating horizontal transfer through worker contact or prey consumption. In empirical tests, insecticide-coated preys selectively killed only two invasive fire ant species (*S. invicta* and *S. geminata*) and a native big-headed ant, *P. morrisii*, while commercial fire ant baits negatively impacted all species tested (Williams *et al.* 1990). This highlights the advantage of prey-baiting in enhancing bait selectivity, which effectively addresses the issue of conventional toxic baits attracting a wide range of ants and/or other animals, leading to potential non-target effects. Prey baiting approach has also been explored for managing the invasive Asian needle ant, *B. chinensis*, a termite specialist that does not appear to use trail pheromone to recruit nestmates to food sources (Bednar & Silverman 2011). Studies have shown that *B. chinensis* can be effectively controlled using insecticide-coated termites, due to their strong preference for termites and their behavioral dominance over other ant species competing for the treated prey (Buczkowski 2016, 2017). Similarly, insecticide-treated termites were effective in controlling *L. humile* in environments where other ant species co-occur (Buczkowski *et al.* 2018). To develop a more practical approach for management programs based on the prey-baiting method, a recent advancement involved mimicking the effect of insect prey by coating granular baits with termite cuticular extracts (Buczkowski 2023). Insecticide-coated prey baits provide a species-specific management option that reduces non-target impacts and enhances control efficacy. This strategy is particularly valuable for invasive ant species that lack trail pheromones, where pheromone-assisted control methods are not viable.

RNA INTERFERENCE

RNA interference (RNAi) is an emerging biorational pest management tool targeting critical genes by delivering double-stranded RNA (dsRNA) that triggers enzymatic degradation of matching messenger RNA (Cooper *et al.* 2019; Taning *et al.* 2020). While a few successful cases against solitary insects exist (Singh *et al.* 2017), the application of RNAi in ant management is less common (Yan *et al.* 2020; Allen 2021). Delivering dsRNA is a major challenge for RNAi techniques in ant management due to the complexity of the food-processing system within an ant colony, which may prevent dsRNA from reaching all castes (e.g., foragers, nurses, broods, and queen) before degradation (Wang *et al.* 2016; Allen 2021). Despite limited case studies, current evidence highlights the potential of RNAi for invasive ant control. In *S. invicta*, nurse workers fed with a dsRNA-containing sucrose solution were able to transfer dsRNA to larvae, leading to molting failure and increased mortality. This was achieved through the silencing of genes involved in pheromone biosynthesis, chemosensory function, and neuropeptide signaling (Choi & Vander Meer 2012; Castillo Bravo 2015; Cheng *et al.* 2015). In *N. fulva*, a study tested dsRNA targeting six housekeeping genes, but only two of them induced significantly higher mortality compared to controls, indicating that not all housekeeping genes are equally effective targets for RNAi-based control (Meng *et al.* 2020). An innovative RNAi method was also developed for *L. humile* to silence immune-related genes in an effort to enhance pathogen transmission; however, the results showed inconsistent effects on pathogen load (Felden *et al.* 2023).

Recent advancements, such as liposome-encapsulated dsRNA, have significantly enhanced RNAi effectiveness by improving its persistence in the gut environment (Yao *et al.* 2022; Wang *et al.* 2024). For practical application, one may consider integrating dsRNA into ant baits to test

if the two have synergism. However, factors such as wash-off from irrigation or rainfall, ultraviolet radiation, and microbial degradation must be addressed as these conditions can break down dsRNA before ants forage on it (Dalakouras *et al.* 2024). To tackle these issues, nanocarriers like chitosan have shown great promise for stabilizing dsRNA under field conditions (Zhou *et al.* 2023). Additionally, bacterially expressed dsRNA may offer a cost-effective alternative, with recent findings demonstrating that liposome-encapsulated bacterial and synthetic dsRNA can achieve similar levels of RNAi efficiency in different invasive ants (Meng *et al.* 2020; Wang *et al.* 2024).

VIRAL PATHOGENS

Viral infections in ants are generally chronic and asymptomatic (Baty *et al.* 2020). The three most studied viruses are likely those positive-sense single-stranded RNA viruses that infect *Solenopsis* spp. (Porter *et al.* 2015): Solenopsis invicta virus-1 (SINV-1 (Valles *et al.* 2004)), Solenopsis invicta virus-2 (SINV-2) (Valles *et al.* 2007), Solenopsis invicta virus-3 (SINV-3) (Valles & Hashimoto 2009). Instead of causing direct mortality, SINV-1 and SINV-2 infections result in reduced foraging, reduced queen weight (SINV-1) and lower fecundity (SINV-2) (Manfredini *et al.* 2016; Hsu *et al.* 2018). All these viruses are highly genus specific and replicate only in *Solenopsis* spp. (Valles 2012; Porter *et al.* 2013; Baty *et al.* 2020). Among these viruses, SINV-3 garnered significant attention for its biological control potential due to its relatively high virulence. Studies have shown that SINV-3 can cause larval and worker mortality as well as reduce queen weight and egg production (Porter *et al.* 2013; Valles *et al.* 2013, 2014). A key challenge in scaling up the field application of viral control is the development of effective virus delivery systems. Studies have demonstrated that microencapsulation techniques such as sodium alginate and hydrogels serve as effective delivery systems for viruses targeting *S. invicta* and other invasive ants including *P. megacephala* and *W. auropunctata* (Tufts *et al.* 2011; Lawrence 2024). In laboratory settings, SINV-3 has been successfully transmitted via sucrose solution and cricket debris paste (Valles *et al.* 2013). Subsequently, field studies in California demonstrated successful inoculation of fire ant populations with SINV-3 via inserting cotton-plug tubes filled with SINV-3 homogenate with sucrose solution, marking the first human-assisted establishment of SINV-3 in the field (Valles & Oi 2014; Oi *et al.* 2019). Another major challenge in microbial control of ants is often their behavioral responses to pathogens or parasites, such as avoidance, grooming, and dispersal, which potentially reduce control effectiveness due to insufficient exposure to pathogens or parasites (Oi & Pereira 1993). However, research indicates that ants do not exhibit such defensive behaviors against viral pathogens, highlighting its suitability as a microbial control agent (Oi & Valles 2009; Liu *et al.* 2025). Despite this advantage, a notable virus-induced behavioral change that warrants further investigation is the reduction in foraging intensity, which may negatively impact baiting efficiency due to inadequate bait consumption. For example, SINV-3-infected *S. invicta* colonies have shown lower levels of bait responsiveness and colony elimination rates compared to non-infected conspecifics (Liu *et al.* 2024; Liu & Yang 2024). Addressing this challenge by restoring foraging activity and improving bait uptake in virus-infected colonies could present a viable strategy to optimize the synergy between virus-based control and conventional baiting strategies. The corresponding author (unpublished data) screened various feeding-stimulating small molecules and identified several that enhance the foraging activity of virus-infected fire ants.

OTHER METHODS TO INCREASE SPECIES SPECIFICITY

Significant efforts are devoted to the development of invasive ant management tools to

increase species specificity such as using ants' own chemicals (e.g., trail pheromone) to attract target ants. Venom alkaloids in *S. invicta* exhibit multiple biological activities, including roles in communication, defending, antimicrobial action, and territorial marking (Xu & Chen 2023). Incorporating venom alkaloids of *S. invicta* into baits does not affect the feeding behavior of *S. invicta* but can prevent other native ants from competing with *S. invicta*, thereby increasing species specificity (Chen 2024). A novel biorational approach involving species-specific receptor-interference (Receptor-i) approach emerged recently. The development process was initiated from screening bioactive peptides on insect Sf9 cell expressed G-protein-coupled receptors (GPCRs; receptors of neuropeptides). The target-specific GPCR agonists or antagonists were then identified (Choi & Vander Meer 2021). Receptor-i was tested on *S. invicta* targeting pheromone biosynthesis activating neuropeptide receptor (PBAN-R) by feeding assay. The peptide treatment has resulted in significant worker and queen mortality, as well as weight loss in those surviving queens (Chinta *et al.* 2023). While the Receptor-i approach against *S. invicta* is expected to have high species specificity, non-target effects have not been examined. Future assessments of Receptor-i should be conducted to determine the optimal delivery methods in the field and potential non-target effects.

SCALABLE AUTOMATED DETECTION AND TREATMENT SYSTEMS

The early detection and surveillance of invasive ants in the field are essential for rapid treatment programs but usually fall short due to their labor-intensive nature (Simberloff 2003; McLaughlin & Dearden 2019). The fire ant eradication program in Australia has integrated various aerial monitoring methods to increase the program's cost-effectiveness (Spring *et al.* 2017). Advanced automated remote detection approaches have recently been implemented by incorporating computer vision techniques and deep learning algorithms with trap stations, unmanned aerial vehicles (UAVs) or robotic dog (dos Santos *et al.* 2022; Su *et al.* 2024; Lin & Lin 2025; Monsimet *et al.* 2025). Additionally, automated aerial baiting using drones and helicopters have also been evaluated and proven to be effective in delivering granular and hydrogel baits (Hoffmann *et al.* 2023; Lin & Lin 2025). Another innovative way to enhance invasive ant detection is a citizen science program in Taiwan in which the public is encouraged to take photos of ants visiting traps consisting of potato chip lures and upload these photos to a reporting platform using a smartphone application. The photos are then analyzed by an AI image recognition system and turned into valuable observation data that facilitate the mapping of invasive ants including *S. invicta* (Lin & Lin 2025).

SYNTHESIS

In this review, we outlined novel invasive ant management strategies and their optimal applications to address different field challenges in various settings (Table 2). Recent advances in management approaches improve species specificity and reduce labor intensity, enhancing the sustainability of invasive ant control. While various tools are available, greater efforts should focus on synergizing these approaches to enhance combined efficacy and resource efficiency. For instance, integrating toxic baits, species-specific pheromones, and microbial control agents into hydrogel formulations may optimize outcomes. We also identified two critical gaps: (1) Regular monitoring of the invasive ant population dynamic is critical for implementing adaptive management strategies that respond to fluctuating population pressures and environmental conditions (Fig. 1). When invasive ants are widespread with high population densities, toxic baits are likely the most effective management tool as baits would be predominantly occupied and consumed by the invasive ants, resulting in minimal and potentially recoverable non-target effects. As invasive ant populations decline, the use of species-specific tools can further mitigate

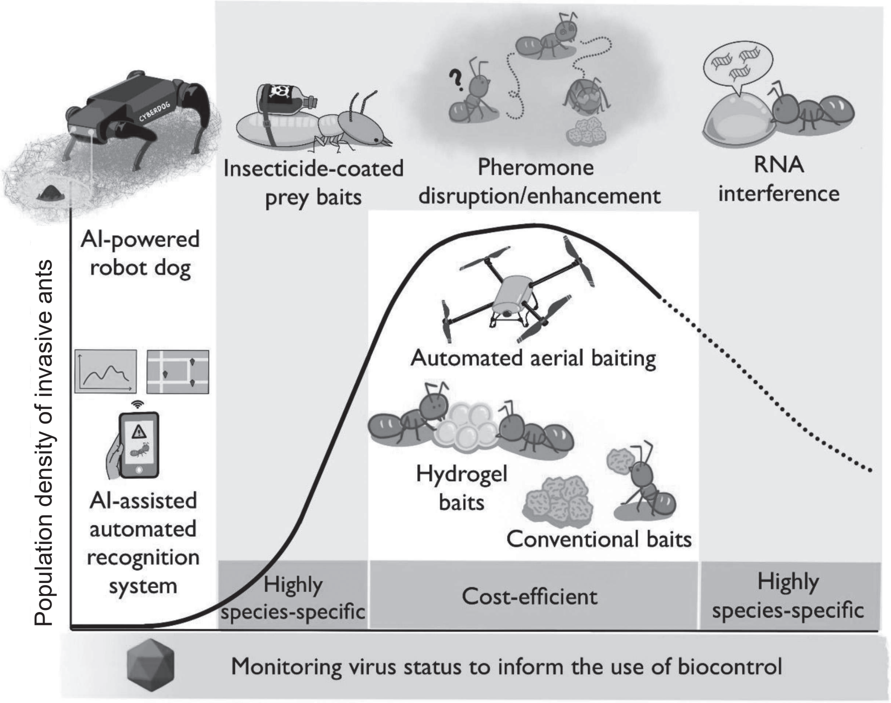

Fig. 1. Adaptive invasive ant management strategies in response to varying population densities and associated environmental conditions.

pressure deriving from non-target effects and support ecosystem recovery. (2) Understanding the often-overlooked role of microbes in ant ecology and behavior may further boost control efficiency as microbial associations can influence ant immunity, foraging, and susceptibility to additional pathogens. To conclude, integrating innovative tools with established strategies represents the key to developing a sustainable, adaptive invasive ant management framework capable of addressing future challenges.

ACKNOWLEDGMENTS

The authors thank the two anonymous reviewers for their constructive comments on an earlier version of the manuscript. This work was supported by the Virginia Agricultural Experiment Station Grant (VA-160193) (Chin-Cheng Scotty Yang; CCSY), Virginia Tech New Faculty Start-up Funds (CCSY), and Virginia Agricultural Council Grant (CCSY).

REFERENCES

Allen, M. L. 2021. Prospects for using RNAi as control for ants. Front. Agron. 3:591539. doi:10.3389/fagro.2021.591539

Angulo, E., B. D. Hoffmann, L. Ballesteros-Mejia, A. Taheri, P. Balzani, A. Bang, ... F. Courchamp. 2022. Economic costs of invasive alien ants worldwide. Biol. Invasions 24:2041–2060. doi:10.1007/s10530-022-02791-w

Baty, J. W., M. Bulgarella, J. Dobelmann, A. Felden, and P. J. Lester. 2020. Viruses and their effects in ants (Hymenoptera: Formicidae). Myrmecol. News 30:213–228. doi:10.25849/myrmecol.news_030:213

Bednar, D. M. and J. Silverman. 2011. Use of termites, *Reticulitermes virginicus*, as a springboard in the invasive success of a predatory ant, *Pachycondyla* (= *Brachyponera*) *chinensis*. Insectes Soc. 58:459–467. doi:10.1007/s00040-011-0163-0

Bertelsmeier, C., S. Ollier, A. Liebhold, and L. Keller. 2017. Recent human history governs global ant invasion dynamics. Nat. Ecol. Evol. 1:0184. doi:10.1038/s41559-017-0184

Boser, C. L., C. Hanna, K. R. Faulkner, C. Cory, J. M.

Randall, and S. A. Morrison. 2014. Argentine ant management in conservation areas: Results of a pilot study. Monogr. West. N. Am. Nat. 7:518–530. doi:10.3398/042.007.0140

Buczkowski, G. 2016. The Trojan horse approach for managing invasive ants: A study with Asian needle ants, *Pachycondyla chinensis*. Biol. Invasions 18:507–515. doi:10.1007/s10530-015-1023-z

Buczkowski, G. 2017. Prey-baiting as a conservation tool: Selective control of invasive ants with minimal non-target effects. Insect Conserv. Divers. 10:302–309. doi:10.1111/icad.12230

Buczkowski, G. 2020. Hydrogel baits pose minimal risk to non-target insects and beneficial species. Entomol. Exp. Appl. 168:948–955. doi:10.1111/eea.12994

Buczkowski, G. 2023. Termite cuticular extracts improve acceptance of bait for controlling invasive Asian needle ants, *Brachyponera chinensis*. Pest Manag. Sci. 79:4004–4010. doi:10.1002/ps.7601

Buczkowski, G. 2024. Insecticide treatment of invasive ant colonies leads to secondary ant invasions and promotes the spread of invasive ants. Biol. Invasions 26:3405–3415. doi:10.1007/s10530-024-03392-5

Buczkowski, G., N. Mothapo, and T. Wossler. 2018. Let them eat termites- Prey-baiting provides effective control of Argentine ants, *Linepithema humile*, in a biodiversity hotspot. J. Appl. Entomol. 142:504–512. doi:10.1111/jen.12501

Buczkowski, G., M. E. Scharf, C. R. Ratliff, and G. W. Bennett. 2005. Efficacy of simulated barrier treatments against laboratory colonies of pharaoh ant. J. Econ. Entomol. 98:485–492. doi:10.1093/jee/98.2.485

Cabrera, E., I. Rivas Fontan, B. D. Hoffmann, and R. Josens. 2021. Laboratory and field insights into the dynamics and behavior of Argentine ants, *Linepithema humile*, feeding from hydrogels. Pest Manag. Sci. 77:3250–3258. doi:10.1002/ps.6368

Castillo Bravo, P. A. 2015. Short neuropeptide F receptor in the worker brain of the red imported fire ant (*Solenopsis invicta* Buren) and methodology for RNA interference. Doctoral dissertation. Department of Entomology, Texas A&M University, Texas, USA. 166 pp.

Cavill, G. W. K., P. L. Robertson, and N. W. Davies. 1979. An Argentine ant aggregation factor. Experientia 35:989–990. doi:10.1007/BF01949898

Chen, J. 2024. A new approach for enhancing ant bait specificity. p.52. *in*: Proceeding of the National Conference on Urban Entomology & Invasive Pest Ant Conference. May 19–22, 2024. Mobile, AL. National Conference on Urban Entomology & Invasive Pest Ant Conference. Durham, NC.

Cheng, D., Y. Lu, L. Zeng, G. Liang, and X. He. 2015. *Si-CSP9* regulates the integument and moulting process of larvae in the red imported fire ant, *Solenopsis invicta*. Sci. Rep. 5:9245. doi:10.1038/srep09245

Chinta, S., R. Vander Meer, E. O'Reilly, and M. Y. Choi. 2023. Insecticidal effects of receptor-interference isolated bioactive peptides on fire ant colonies. Int. J. Mol. Sci. 24:13978. doi:10.3390/ijms241813978

Choe, D. H. and M. K. Rust. 2008. Horizontal transfer of insecticides in laboratory colonies of the Argentine ant (Hymenoptera: Formicidae). J. Econ. Entomol. 101:1397–1405. doi:10.1093/jee/101.4.1397

Choe, D. H., J. W. Tay, K. Campbell, H. Park, L. Greenberg, and M. K. Rust. 2021. Development and demonstration of low-impact IPM strategy to control Argentine ants (Hymenoptera: Formicidae) in urban residential settings. J. Econ. Entomol. 114:1752–1757. doi:10.1093/jee/toab079

Choe, D. H., K. Tsai, C. M. Lopez, and K. Campbell. 2014. Pheromone-assisted techniques to improve the efficacy of insecticide sprays against *Linepithema humile* (Hymenoptera: Formicidae). J. Econ. Entomol. 107:319–325. doi:10.1603/EC13262

Choi, M. Y. and R. K. Vander Meer. 2012. Ant trail pheromone biosynthesis is triggered by a neuropeptide hormone. PLOS ONE 7:e50400. doi:10.1371/journal.pone.0050400

Choi, M. Y. and R. K. Vander Meer. 2021. GPCR-based bioactive peptide screening using phage-displayed peptides and an insect cell system for insecticide discovery. Biomolecules 11:583. doi:10.3390/biom11040583

Cooper, A. M., K. Silver, J. Zhang, Y. Park, and K. Y. Zhu. 2019. Molecular mechanisms influencing efficiency of RNA interference in insects. Pest Manag. Sci. 75:18–28. doi:10.1002/ps.5126

Dalakouras, A., V. Koidou, and K. Papadopoulou. 2024. DsRNA-based pesticides: Considerations for efficiency and risk assessment. Chemosphere 352:141530. doi:10.1016/j.chemosphere.2024.141530

Davis, P. and J. van Schagen. 1993. Effective control of pest ants. J. Dept. Agric. Western Australia 34:92–97.

Diagne, C., B. Leroy, A. C. Vaissière, R. E. Gozlan, D. Roiz, I. Jarić, ... F. Courchamp. 2021. High and rising economic costs of biological invasions worldwide. Nature 592:571–576. doi:10.1038/s41586-021-03405-6

dos Santos, A., B. J. G. Biesseck, N. Latte, I. C. de Lima Santos, W. P. dos Santos, R. Zanetti, and J. C. Zanuncio. 2022. Remote detection and measurement

of leaf-cutting ant nests using deep learning and an unmanned aerial vehicle. Comput. Electron. Agric. 198:107071. doi:10.1016/j.compag.2022.107071

Edwards, J. P. 1986. The biology, economic importance, and control of the Pharaoh's ant, *Monomorium pharaonis* (L.). p.257–271. *in*: Economic Impact and Control of Social Insects. (Vinson, S. B., ed.) Praeger. New York, NY. 421 pp.

Felden, A., J. Dobelmann, J. W. Baty, J. McCormick, J. Haywood, and P. J. Lester. 2023. Can immune gene silencing via dsRNA feeding promote pathogenic viruses to control the globally invasive Argentine ant? Ecol. Appl. 33:e2755. doi:10.1002/eap.2755

Folgatait, P. J. and L. E. Gilbert. 1999. Phorid parasitoids affect foraging activity of *Solenopsis richteri* under different availability of food in Argentina. Ecol. Entomol. 24:163–173. doi:10.1046/j.1365-2311.1999.00180.x

Gan, J., S. Bondarenko, L. Oki, D. Haver, and J. Li. 2012. Occurrence of fipronil and its biologically active derivatives in urban residential runoff. Environ. Sci. Technol. 46:1489–1495. doi:10.1021/es202904x

Greenberg, L. and J. H. Klotz. 2000. Argentine ant (Hymenoptera: Formicidae) trail pheromone enhances consumption of liquid sucrose solution. J. Econ. Entomol. 93:119–122. doi:10.1603/0022-0493-93.1.119

Greenberg, L., M. K. Rust, J. H. Klotz, D. Haver, J. N. Kabashima, S. Bondarenko, and J. Gan. 2010. Impact of ant control technologies on insecticide runoff and efficacy. Pest Manag. Sci. 66:980–987. doi:10.1002/ps.1970

Haddi, K., L. M. Turchen, L. O. Viteri Jumbo, R. N. C. Guedes, E. J. G. Pereira, R. W. S. Aguiar, and E. E. Oliveira. 2020. Rethinking biorational insecticides for pest management: Unintended effects and consequences. Pest Manag. Sci. 76:2286–2293. doi:10.1002/ps.5837

Hoefele, D., J. M. Chalissery, R. Gries, and G. Gries. 2020. Effects of trail pheromone purity, dose, and type of placement on recruiting European fire ants, *Myrmica rubra*, to food baits. J. Entomol. Soc. Brit. Columbia 117:31–41.

Hoffmann, B. D. 2023. Honey bees are not attracted to multiple new ant bait matrices containing sugar. Bull. Entomol. Res. 113:190–195. doi:10.1017/S0007485322000451

Hoffmann, B. D., A. Tessmann, G. Quinn, and F. Lawton. 2023. Quantification of flight times of aerial treatments targeting invasive species: The interplay of helicopter or drone with bait-delivery systems, flight speed and bait form. Pest Manag. Sci. 79:2050–2055. doi:10.1002/ps.7379

Hoffmann, B. D., G. M. Luque, C. Bellard, N. D. Holmes, and C. J. Donlan. 2016. Improving invasive ant eradication as a conservation tool: A review. Biol. Conserv. 198:37–49. doi:10.1016/j.biocon.2016.03.036

Holway, D. A., L. Lach, A. V. Suarez, N. D. Tsutsui, and T. J. Case. 2002. The causes and consequences of ant invasions. Annu. Rev. Ecol. Syst. 33:181–233. doi:10.1146/annurev.ecolsys.33.010802.150444

Hsu, H. W., M. C. Chiu, D. Shoemaker, and C. C. S. Yang. 2018. Viral infections in fire ants lead to reduced foraging activity and dietary changes. Sci. Rep. 8:13498. doi:10.1038/s41598-018-31969-3

Jiang, W., A. Soeprono, M. K. Rust, and J. Gan. 2014. Ant control efficacy of pyrethroids and fipronil on outdoor concrete surfaces. Pest Manag. Sci. 70:271–277. doi:10.1002/ps.3555

Josens, R., A. Mattiacci, J. Lois-Milevicich, and A. Giacometti. 2016. Food information acquired socially overrides individual food assessment in ants. Behav. Ecol. Sociobiol. 70:2127–2138. doi:10.1007/s00265-016-2216-x

Kafle, L., W. J. Wu, R. N. Huang, and C. J. Shih. 2015. Effects of moisture on the efficacy of fire ant *Solenopsis invicta* Buren (Hymenoptera: Formicidae) baits, 2012. Arthropod Manag. Tests 40:L6. doi:10.1093/amt/tsv202

Kafle, L., W. J. Wu, and C. J. Shih. 2010. A new fire ant (Hymenoptera: Formicidae) bait base carrier for moist conditions. Pest Manag. Sci. 62:1082–1088. doi:10.1002/ps.1981

Klotz, J. H. 2010. Urban Pest Management of Ants in California. Vol. 3524. UC Agriculture and Natural Resources. Oakland, CA. 72 pp.

Klotz, J. H., L. Greenberg, H. H. Shorey, and D. F. Williams. 1997. Alternative control strategies for ants around homes. J. Agric. Entomol. 14:249–257.

Klotz, J. H., J. R. Mangold, K. M. Vail, L. R. Davis Jr., and R. S. Patterson. 1995. A survey of the urban pest ants (Hymenoptera: Formicidae) of peninsular Florida. Fla. Entomol. 78:109–118. doi:10.2307/3495674

Klotz, J. H., M. K. Rust, L. Greenberg, H. C. Field, and K. Kupfer. 2007. An evaluation of several urban pest management strategies to control Argentine ants (Hymenoptera: Formicidae). Sociobiology 50:391–398.

Knight, R. L. and M. K. Rust. 1990. Repellency and efficacy of insecticides against foraging workers in laboratory colonies of Argentine ants (Hymenoptera: Formicidae). J. Econ. Entomol. 83:1402–1408. doi:10.1093/jee/83.4.1402

Krushelnycky, P. D. and N. J. Reimer. 1998. Bait prefer-

ence by the Argentine ant (Hymenoptera: Formicidae) in Haleakala National Park, Hawaii. Environ. Entomol. 27:1482–1487. doi:10.1093/ee/27.6.1482

Lawrence, J. A. 2024. Community ecology of two pest ant species in Hawai‘i and a potential advancement in microbial ant biocontrol. Master Thesis. Department of Entomology, University of Hawai‘i at Manoa, Hawai‘i, USA. 48 pp.

Le, B., H. Park, K. Campbell, M. K. Rust, C. Y. Lee, and D. H. Choe. 2023. Laboratory evaluations of biodegradable boric acid hydrogel baits for the control of Argentine ant (Hymenoptera: Formicidae). J. Econ. Entomol. 116:643–647. doi:10.1093/jee/toad037

Lee, C. C., M. Y. Lu, J. T. C. Chen, J. W. Tay, C. C. S. Yang, and C. C. Lin. 2025. Development of alginate hydrogel baits for the management of longlegged ant (Hymenoptera: Formicidae). J. Econ. Entomol. 118:838–845. doi:10.1093/jee/toaf011

Lin, H. M. and C. C. Lin. 2025. Pioneering control technologies for red imported fire ants (*Solenopsis invicta*) in Taiwan. Glob. Environ. Res. 28:143–150.

Liu, F. L. C., K. Ivanov, and C. C. S. Yang. 2024. Invasive alien ants in the United States: Current status and countermeasures. Glob. Environ. Res. 28:171–178.

Liu, F. L. C., W. J. Lin, L. McMillan, and C. C. S. Yang. 2025. Fire ants exhibit self-medication but lack preventive behavioral immunity against a viral pathogen. J. Invertebr. Pathol. 211:108339. doi:10.1016/j.jip.2025.108339

Liu, F. L. and C. C. S. Yang. 2024. SINV-infected fire ants are less responsive to baiting. p.25. *in*: Proceeding of the National Conference on Urban Entomology & Invasive Pest Ant Conference. May 19–22, 2024. Mobile, AL. National Conference on Urban Entomology & Invasive Pest Ant Conference. Durham, NC.

Loke, P. Y. and C. Y. Lee. 2004. Foraging behavior of field populations of the big-headed ant, *Pheidole megacephala* (Hymenoptera: Formicidae). Sociobiology 43:211–220.

Manfredini, F., D. Shoemaker, and C. M. Grozinger. 2016. Dynamic changes in host-virus interactions associated with colony founding and social environment in fire ant queens (*Solenopsis invicta*). Ecol. Evol. 6:233–244. doi:10.1002/ece3.1843

McCalla, K. A., J. W. Tay, A. Mulchandani, D. H. Choe, and M. S. Hoddle. 2020. Biodegradable alginate hydrogel bait delivery system effectively controls high-density populations of Argentine ant in commercial citrus. J. Pest Sci. 93:1031–1042. doi:10.1007/s10340-019-01175-9

McLaughlin, G. M. and P. K. Dearden. 2019. Invasive insects: Management methods explored. J. Insect Sci. 19:17. doi:10.1093/jisesa/iez085

Meng, J., J. Lei, A. Davitt, J. R. Holt, J. Huang, R. Gold, ... K. Zhu-Salzman. 2020. Suppressing tawny crazy ant (*Nylanderia fulva*) by RNAi technology. Insect Sci. 27:113–121. doi:10.1111/1744-7917.12604

Milosavljević, I., N. A. Irvin, M. Lewis, and M. S. Hoddle. 2024. Spinosad-infused biodegradable hydrogel beads as a potential organic approach for argentine ant, *Linepithema humile* (Mayr) (Hymenoptera: Formicidae), management in California citrus orchards. J. Appl. Entomol. 148:117–127. doi:10.1111/jen.13203

Monsimet, J., S. Sjögersten, N. J. Sanders, M. Jonsson, J. Olofsson, and M. Siewert. 2025. UAV data and deep learning: Efficient tools to map ant mounds and their ecological impact. Remote Sens. Ecol. Conserv. 11:5–19. doi:10.1002/rse2.400

Neff, R., R. T. Puckett, and R. E. Gold. 2011. Particle size and bait preference of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). Sociobiology 58:473–488.

Nishisue, K., E. Sunamura, Y. Tanaka, H. Sakamoto, S. Suzuki, T. Fukumoto, ... S. Tatsuki. 2010. Long-term field trial to control the invasive Argentine ant (Hymenoptera: Formicidae) with synthetic trail pheromone. J. Econ. Entomol. 103:1784–1789. doi:10.1603/EC10008

Oi, D. H., R. A. Atchison, G. Chuzel, J. Chen, J. A. Henke, and R. D. Weeks. 2022a. Effect of irrigation on the control of red imported fire ants (Hymenoptera: Formicidae) by water-resistant and standard fire ant baits. J. Econ. Entomol. 115:266–272. doi:10.1093/jee/toab242

Oi, D. H., A. Lucky, and D. M. Liebowitz. 2022b. Response of *Wasmannia auropunctata* (Hymenoptera: Formicidae) to water-soaked imported fire ant baits. Fla. Entomol. 105:108–114. doi:10.1653/024.105.0202

Oi, D. H. and F. M. Oi. 2006. Speed of efficacy and delayed toxicity characteristics of fast-acting fire ant (Hymenoptera: Formicidae) baits. J. Econ. Entomol. 99:1739–1748. doi:10.1093/jee/99.5.1739

Oi, D. H. and R. M. Pereira. 1993. Ant behavior and microbial pathogens (Hymenoptera: Formicidae). Fla. Entomol. 76:63–74. doi:10.2307/3496014

Oi, D. H. and S. Valles. 2009. Fire ant control with entomopathogens in the USA. p.237–257. *in*: Use of Microbes for Control and Eradication of Invasive Arthropods. Progress in Biological Control. Vol. 6. (Hajek, A. E., T. R. Glare, and M. O'Callaghan, eds.) Springer. Dordrecht, The Netherlands. 365 pp. doi:10.1007/978-1-4020-8560-4_13

Oi, D. H., S. Valles, S. Porter, C. Cavanaugh, G. White,

and J. Henke. 2019. Introduction of fire ant biological control agents into the Coachella Valley of California. Fla. Entomol. 102:284–286.

Orr, M. R. and S. H. Seike. 1998. Parasitoids deter foraging by Argentine ants (*Linepithema humile*) in their native habitat in Brazil. Oecologia 117:420–425. doi:10.1007/s004420050676

Peck, R. W., K. Donmoyer, K. Scheiner, R. Karimi, and S. Kropidlowski. 2017. Efforts to Eradicate Yellow Crazy Ants on Johnston Atoll: Results from Crazy Ant Strike Teams X, XI, and XII (June 2015–December 2016). Technical Report HCSU-081. Hawai‘i Cooperative Studies Unit, University of Hawai‘i at Hilo. Hilo, HI. 28 pp.

Porter, S. D., S. M. Valles, and D. H. Oi. 2013. Host specificity and colony impacts of the fire ant pathogen, Solenopsis invicta virus 3. J. Invertebr. Pathol. 114:1–6. doi:10.1016/j.jip.2013.04.013.

Porter, S. D., S. M. Valles, A. L. Wild, R. Dieckmann, and N. J. Plowes. 2015. Solenopsis invicta virus 3: Further host-specificity tests with native *Solenopsis* ants (Hymenoptera: Formicidae). Fla. Entomol. 98:122–125. doi:10.1653/024.098.0120

Roy, H. E., A. Pauchard, P. Stoett, T. R. Truong, S. Bacher, B. S. Galil, ... M. A. McGeoch. 2023. IPBES invasive alien species assessment: Summary for policymakers. IPBES secretariat. Bonn, Germany. 52 pp. doi:10.5281/zenodo.10127924

Rust, M. K., D. A. Reierson, and J. H. Klotz. 2004. Delayed toxicity as a critical factor in the efficacy of aqueous baits for controlling Argentine ants (Hymenoptera: Formicidae). J. Econ. Entomol. 97:1017–1024. doi:10.1093/jee/97.3.1017

Rust, M. K., D. A. Reierson, E. Paine, and L. J. Blum. 2000. Seasonal activity and bait preferences of the Argentine ant (Hymenoptera: Formicidae). J. Agric. Urban Entomol. 17:201–212.

Rust, M. K., A. Soeprono, S. Wright, L. Greenberg, D. H. Choe, C. L. Boser, ... C. Hanna. 2015. Laboratory and field evaluations of polyacrylamide hydrogel baits against Argentine ants (Hymenoptera: Formicidae). J. Econ. Entomol. 108:1228–1236. doi:10.1093/jee/tov044

Sakamoto, Y., T. I. Hayashi, M. N. Inoue, H. Ohnishi, T. Kishimoto, and K. Goka. 2019. Effects of fipronil on non-target ants and other invertebrates in a program for eradication of the Argentine ant, *Linepithema humile*. Sociobiology 66:227–238. doi:10.13102/sociobiology.v66i2.3772

Sardain, A., E. Sardain, and B. Leung. 2019. Global forecasts of shipping traffic and biological invasions to 2050. Nat. Sustain. 2:274–282. doi:10.1038/s41893-019-0245-y

Sidhu, C. S. and E. E. Wilson Rankin. 2016. Honey bees avoiding ant harassment at flowers using scent cues. Environ. Entomol. 45:420–426. doi:10.1093/ee/nvv230

Simberloff, D. 2003. How much information on population biology is needed to manage introduced species? Conserv. Biol. 17:83–92. doi:10.1046/j.1523-1739.2003.02028.x

Singh, I. K., S. Singh, K. Mogilicherla, J. N. Shukla, and S. R. Palli. 2017. Comparative analysis of double-stranded RNA degradation and processing in insects. Sci. Rep. 7:17059. doi:10.1038/s41598-017-17134-2

Soeprono, A. M. and M. K. Rust. 2004. Effect of horizontal transfer of barrier insecticides to control Argentine ants (Hymenoptera: Formicidae). J. Econ. Entomol. 97:1675–1681. doi:10.1603/0022-0493-97.5.1675

Spring, D., L. Croft, and T. Kompas. 2017. Look before you treat: Increasing the cost effectiveness of eradication programs with aerial surveillance. Biol. Invasions 19:521–535. doi:10.1007/s10530-016-1292-1

Su, X., G. Shi, J. Zhong, Y. Li, W. Dai, A. G. Xu, ... Z. Yan. 2024. The implementation of robotic dogs in automatic detection and surveillance of red imported fire ant nests. Pest Manag. Sci. 80:5277–5285. doi:10.1002/ps.8254

Suckling, D., R. Peck, L. Manning, L. Stringer, J. Cappadonna, and A. El-Sayed. 2008. Pheromone disruption of Argentine ant trail integrity. J. Chem. Ecol. 34:1602–1609. doi:10.1007/s10886-008-9566-4

Suckling, D. M., L. D. Stringer, B. Bunn, A. M. El-Sayed, and R. K. Vander Meer. 2010. Trail pheromone disruption of red imported fire ant. J. Chem. Ecol. 36:744–750. doi:10.1007/s10886-010-9810-6

Suckling, D. M., L. D. Stringer, J. E. Corn, B. Bunn, A. M. El-Sayed, and R. K. Vander Meer. 2012. Aerosol delivery of trail pheromone disrupts the foraging of the red imported fire ant, *Solenopsis invicta*. Pest Manag. Sci. 68:1572–1578. doi:10.1002/ps.3349

Sunamura, E. 2018. Application of trail pheromones to management of pest ants. p.159–169. *in*: Chemical Ecology of Insects. (Tabata, J., ed.) CRC Press. Boca Raton, FL. 304 pp. doi:10.1201/9781351228398-7

Sunamura, E., M. Terayama, R. Fujimaki, T. Ono, G. Buczkowski, and K. Eguchi. 2022. Development of an effective hydrogel bait and an assessment of community-wide management targeting the invasive white-footed ant, *Technomyrmex brunneus*. Pest Manag. Sci. 78:4083–4091. doi:10.1002/ps.7027

Tanaka, Y., K. Nishisue, E. Sunamura, S. Suzuki, H. Sakamoto, T. Fukumoto, ... S. Tatsuki. 2009. Trail-fol-

lowing disruption in the invasive Argentine ant with a synthetic trail pheromone component (Z)-9-hexadecenal. Sociobiology 54:139–152.

Taning, C. N., S. Arpaia, O. Christiaens, A. Dietz-Pfeilstetter, H. Jones, B. Mezzetti, ... V. Ventura. 2020. RNA-based biocontrol compounds: Current status and perspectives to reach the market. Pest Manag. Sci. 76:841–845. doi:10.1002/ps.5686

Tay, J. W., D. H. Choe, A. Mulchandani, and M. K. Rust. 2020. Hydrogels: From controlled release to a new bait delivery for insect pest management. J. Econ. Entomol. 113:2061–2068. doi:10.1093/jee/toaa183

Tay, J. W., M. S. Hoddle, A. Mulchandani, and D. H. Choe. 2017. Development of an alginate hydrogel to deliver aqueous bait for pest ant management. Pest Manag. Sci. 73:2028–2038. doi:10.1002/ps.4616

Terayama, M., T. Kankawa, H. Shirai, Y. Tomioka, S. Kohno, K. Matsumoto, ... K. Eguchi. 2025. Field evaluations of a novel biodegradable microfibrillated cellulose hydrogel bait targeting the invasive white-footed ant, *Technomyrmex brunneus*. J. Appl. Entomol. 149:363–371. doi:10.1111/jen.13388

Tufts, D. M., K. Spencer, W. B. Hunter, and B. Bextine. 2011. Delivery system using sodium alginate virus loaded pellets to red imported fire ants (*Solenopsis invicta*, Hymenoptera: Formicidae). Fla. Entomol. 94:237–241. doi:10.1653/024.094.0217

Valles, S. M. 2012. Positive-strand RNA viruses infecting the red imported fire ant, *Solenopsis invicta*. Psyche: J. Entomol. 2012:821591. doi: 10.1155/2012/821591

Valles, S. M. and Y. Hashimoto. 2009. Isolation and characterization of Solenopsis invicta virus 3, a new positive-strand RNA virus infecting the red imported fire ant, *Solenopsis invicta*. Virology 388:354–361. doi:10.1016/j.virol.2009.03.028

Valles, S. M. and D. H. Oi. 2014. Successful transmission of Solenopsis invicta virus 3 to field colonies of *Solenopsis invicta* (Hymenoptera: Formicidae). Fla. Entomol. 97:1244–1246. doi:10.1653/024.097.0334

Valles, S. M., S. D. Porter, M. Y. Choi, and D. H. Oi. 2013. Successful transmission of Solenopsis invicta virus 3 to *Solenopsis invicta* fire ant colonies in oil, sugar, and cricket bait formulations. J. Invertebr. Pathol. 113:198–204. doi:10.1016/j.jip.2013.04.003

Valles, S. M., S. D. Porter, and A. E. Firth. 2014. Solenopsis invicta virus 3: Pathogenesis and stage specificity in red imported fire ants. Virology 460–461:66–71. doi:10.1016/j.virol.2014.04.026

Valles, S. M., C. A. Strong, P. M. Dang, W. B. Hunter, R. M. Pereira, D. H. Oi, ... D. F. Williams. 2004. A picorna-like virus from the red imported fire ant, *Solenopsis invicta*: Initial discovery, genome sequence, and characterization. Virology 328:151–157. doi:10.1016/j.virol.2004.07.016

Valles, S. M., C. A. Strong, and Y. Hashimoto. 2007. A new positive-strand RNA virus with unique genome characteristics from the red imported fire ant, *Solenopsis invicta*. Virology 365:457–463. doi:10.1016/j.virol.2007.03.043

Vander Meer, R. and D. Milne. 2017. Enhanced pest ant control with hydrophobic bait. J. Econ. Entomol. 110:567–574. doi:10.1093/jee/tow300

Vander Meer, R. K., F. Alvarez, and C. S. Lofgren. 1988. Isolation of the trail recruitment pheromone of *Solenopsis invicta*. J. Chem. Ecol. 14:825–838. doi:10.1007/BF01018776

Wang, J. D., Y. H. Chen, Y. X. Zhang, J. W. Lin, S. J. Gao, B. Z. Tang, and Y. M. Hou. 2024. Establishment of RNAi-mediated pest control method for red imported fire ant, *Solenopsis invicta*. J. Agric. Food. Chem. 72:10936–10943. doi:10.1021/acs.jafc.4c00654

Wang, K., Y. Peng, J. Pu, W. Fu, J. Wang, and Z. Han. 2016. Variation in RNAi efficacy among insect species is attributable to dsRNA degradation *in vivo*. Insect Biochem. Mol. Biol. 77:1–9. doi:10.1016/j.ibmb.2016.07.007

Welzel, K. F. and D. H. Choe. 2016. Development of a pheromone-assisted baiting technique for Argentine ants (Hymenoptera: Formicidae). J. Econ. Entomol. 109:1303–1309. doi:10.1093/jee/tow015

Williams, D. 1986. Chemical baits: specificity and effects on other ant species. *in*: Fire Ants and Leaf-cutting Ants. (Lofgren, C. S. and R. K. Vander Meer, eds.) CRC Press. Boca Raton, FL. 416 pp. doi:10.1201/9780429038266-31

Williams, D., C. Lofgren, and R. Vander Meer. 1990. Fly pupae as attractant carriers for toxic baits for red imported fire ants (Hymenoptera: Formicidae). J. Econ. Entomol. 83:67–73. doi:10.1093/jee/83.1.67

Wiltz, B., D. Suiter, and W. Gardner. 2010. Activity of bifenthrin, chlorfenapyr, fipronil, and thiamethoxam against red imported fire ants (Hymenoptera: Formicidae). J. Econ. Entomol. 103:754–761. doi:10.1603/EC09350

Xu, G. and L. Chen. 2023. Biological activities and ecological significance of fire ant venom alkaloids. Toxins 15:439. doi:10.3390/toxins15070439

Yan, S., B. Ren, B. Zeng, and J. Shen. 2020. Improving RNAi efficiency for pest control in crop species. BioTechniques 68:283–290. doi:10.2144/btn-2019-0171

Yao, Y., D. J. Lin, Z. Y. Cai, R. Wang, Y. M. Hou, C. H. Hu, ... J. D. Wang. 2022. Multiple dsRNases involved in exogenous dsRNA degradation of fall armyworm *Spodoptera frugiperda*. Front. Physiol.

13:850022. doi:10.3389/fphys.2022.850022

Zakharov, A. and L. Thompson. 1998. Effects of repeated use of fenoxycarb and hydramethylnon baits on nontarget ants. J. Entomol. Sci. 33:212–220. doi:10.18474/0749-8004-33.2.212

Zanola, D., T. J. Czaczkes, and R. Josens. 2024. Ants evade harmful food by active abandonment. Commun. Biol. 7:84. doi:10.1038/s42003-023-05729-7

Zhou, H., F. Wan, Y. Jian, F. Guo, M. Zhang, S. Shi, ... W. Ding. 2023. Chitosan/dsRNA polyplex nanoparticles advance environmental RNA interference efficiency through activating clathrin-dependent endocytosis. Int. J. Biol. Macromol. 253:127021. doi:10.1016/j.ijbiomac.2023.127021

入侵螞蟻防治新趨勢：創新技術與精準整合策略

劉芳綾 [1] 曾書萍 [2] 林宗岐 [3] 楊景程 [4,*]

摘要

劉芳綾、曾書萍、林宗岐、楊景程。2025。入侵螞蟻防治新趨勢：創新技術與精準整合策略。台灣農業研究 74(2):113–128。

過去入侵螞蟻的防治方法主要依賴餌劑，近年相關研究則朝向更精準、永續及符合經濟效益的方向發展，致力於創新或結合更具物種專一性且環境友善的策略。本綜述著重探討可提升防治效率的新興入侵螞蟻防治方法，例如：水凝膠餌劑、物種專一費洛蒙干擾覓食或促進餌劑取食、殺蟲劑處理之天然食餌以及微生物 (病毒) 防治。此外，本篇亦討論了幾種新興技術與其應用，如 RNA 干擾技術與搭載人工智慧的監測工具。在此篇綜述中，我們概述了各種防治方法在面對不同螞蟻族群密度以及環境因子的優勢與局限性，並提供了這些創新技術如何有效整合於入侵螞蟻的管理策略中。防治人員可依據入侵螞蟻的族群密度制定防治策略，能在族群密度高峰時進行積極防治，而隨著入侵螞蟻密度降低，使用針對該入侵螞蟻的防治方法，一方面保持防治效果並同時支持生態系統恢復，既可以最大化防治效率亦可減少非目標影響。

關鍵詞：入侵螞蟻、餌劑防治、水凝膠、生物合理性防治、人工智慧。

投稿日期：2025 年 1 月 25 日；接受日期：2025 年 4 月 23 日。

* 通訊作者：scottyyang@vt.edu

1 美國維吉尼亞理工大學昆蟲學系博士候選人。美國 維吉尼亞州。

2 國立臺灣大學昆蟲學系助理教授。臺灣 臺北市。

3 國立彰化師範大學生物學系特聘教授。臺灣 彰化市。

4 美國維吉尼亞理工大學昆蟲學系助理教授。美國 維吉尼亞州。

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):129–140 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0003

二氧化碳補充對蝴蝶蘭光合作用及生長開花之影響

蔡明軒 [1,*] 陳葦玲 [2]

摘要

蔡明軒、陳葦玲。2025。二氧化碳補充對蝴蝶蘭光合作用及生長開花之影響。台灣農業研究 74(2):129–140。

蝴蝶蘭 (*Phalaenopsis*) 生產過程設備及能源投入密集，為提升生產及能源利用效率，補充二氧化碳 (CO_2) 為值得評估投入的議題，本文彙整添加 CO_2 應用在蝴蝶蘭栽培中的相關研究。在營養生長時期補充 CO_2 濃度至 700–800 μL L^{-1}，能促進蝴蝶蘭生長速率或生物量，惟氮肥供應不足則影響補充的效益。催花後的生殖生長期補充 CO_2 至 1,000 μL L^{-1} 能縮短抽梗所需日數，或促進花梗數量、花苞數、花梗重量及瓶插壽命等，但部分研究中補充濃度達 1,600 μL L^{-1} 會造成地上部鮮重與乾重減少或花苞掉落。

關鍵詞：二氧化碳增濃、景天酸代謝、生育期、設施。

前言

2023 年臺灣蘭花種植面積 975 ha，以蝴蝶蘭 (*Phalaenopsis*)、文心蘭 (*Oncidium*) 切花及蕙蘭 (*Cymbidium*) 為大宗，年產值達新臺幣 72.1 億元，外銷金額為 61.6 億元，外銷占比超過 85.0%，是我國重要的外銷花卉產業，前三大外銷國際市場依序為美國 (33.8%)、日本 (29.0%) 及越南 (9.0%) (農業 E 報，https://epost.moa.gov.tw/theme_data.php?theme=e-post&sub_theme=photo&id=980)。其中，蝴蝶蘭外銷占比 8 成以上為最大花卉品項，從品種選育、組織培養、小中大苗、催花到盆花及切花生產產業鏈相對完整。然而，蝴蝶蘭生產過程需要投入大量資本控制環境條件，以達到定期定量供應生產，並在此基礎上增加特定設備提升產能，以進一步降低既有設施設備的單位成本，提升整體經濟效益。透過補充二氧化碳 (CO_2) 提升蝴蝶蘭生產效率為可行策略，藉由促進作物光合作用速率，可提高生長速率或開花品質。

以往添加 CO_2 或增濃 (enrichment) 相關研究多著重在 C_3 與 C_4 植物，對於蝴蝶蘭等景天酸代謝 (crassulacean acid metabolism; CAM) 植物的研究則較為缺乏。由於夜間為 CAM 植物吸收 CO_2 主要階段，而當夜間無需通風，或蝴蝶蘭催花至開花期間使用空調降溫時，CO_2 在密閉性高的溫室中可能因光合作用被吸收而短缺。以 CO_2 感測器 (CO_2-9914SD, Lutron Electronic Enterprise Co., Ltd., Taipei, Taiwan) 實際測量結果，顯示催花溫室內夜間 CO_2 濃度與日間之差距可達 200 μL L^{-1} (圖 1)。有鑑於國內業者已開始嘗試加入 CO_2 為環控因子，本文特彙整相關研究結果，以作為後續研發與產業利用之參考。

CO_2 與植物光合作用之關係

大氣中的 CO_2 為植物行光合作用所需的主要碳源，當 CO_2 進入葉肉細胞後，核酮糖-1,5-二磷酸羧化/加氧酶 (ribulose-1,5-bisphosphate carboxylase/oxygenase; Rubisco) 催化 CO_2 與核酮糖-1,5-二磷酸 (ribulose-1,5-bisphosphate; RuBP) 結合，稱為羧化反應 (carboxylation)，

投稿日期：2024 年 12 月 5 日；接受日期：2025 年 2 月 11 日。
[*] 通訊作者：krill1318@gmail.com
[1] 農業部農業試驗所花卉試驗分所產業應用系助理研究員。臺灣 雲林縣。
[2] 農業部農業試驗所花卉試驗分所產業應用系副研究員兼系主任。臺灣 雲林縣。

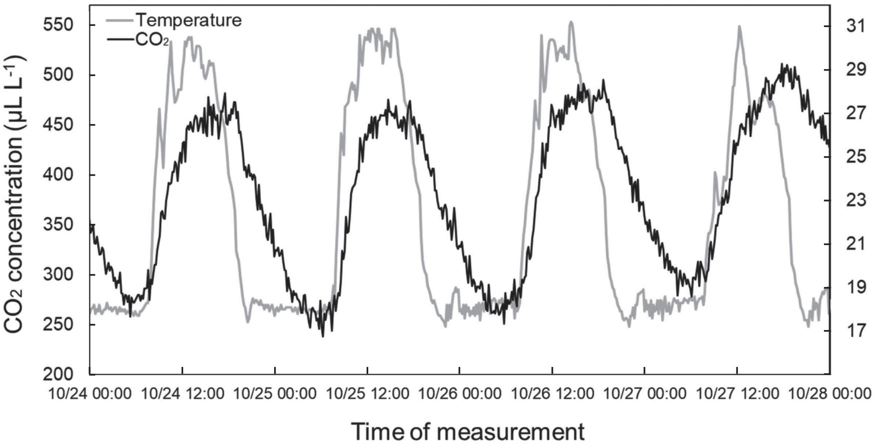

圖 1. 2024 年 10 月 24–28 日期間位於嘉義縣大林鎮之蝴蝶蘭催花溫室內 CO_2 濃度日變化。

Fig. 1. Diurnal variation of carbon dioxide (CO_2) concentration in a *Phalaenopsis* flower-forcing greenhouse located in Dalin Township, Chiayi County from October 24 to 28, 2024.

然後進入卡爾文循環 (Calvin cycle) 轉化為碳水化合物。CAM 植物主要透過磷酸烯醇丙酮酸羧化酶 (phosphoenolpyruvate carboxylase; PEPC) 促使 CO_2 轉換為蘋果酸 (malic acid) 貯存於液胞，日間 CO_2 被釋放進入卡爾文循環 (Osmond 1978; Roberts *et al*. 1997) (圖 2)。

當環境中 CO_2 濃度升高時能促進羧化反應速率，Rubisco 亦能催化 RuBP 與氧氣 (O_2) 結合而釋放 CO_2，稱為光呼吸作用 (photorespiration)。此反應會降低光合作用的固碳效率，透過提高環境中 CO_2 濃度，能使之與 O_2 競爭 Rubisco 上之結合位，抑制光呼吸作用，故不論是促進羧化反應或是抑制光呼吸作用，結果都能提升淨光合作用速率 (Bowes 1991; Makino & Mae 1999)。不過長時間提高 CO_2 濃度對光合作用速率可能發生回饋抑制 (feedback inhibition)，或因馴化 (acclimation) 而下調 (Sage 1994; Moore *et al*. 2002; Wolfe *et al*. 2002; Bunce & Sicher 2003; Qian *et al*. 2012)，因此補充 CO_2 時須考量物種種類、作物發育階段及環境光度與溫度等條件。

蝴蝶蘭光合作用之特性

蝴蝶蘭瓶苗時為 C_3-CAM 植物，出瓶後小、中及大苗則為典型的絕對型 CAM 植物 (Hung 2012)。CAM 植物的光合作用依其特性，通常可在一個日夜週期中分為 4 個階段 (phase) (圖 3A)。以蝴蝶蘭為例：phase-I 發生於暗期，隨光期開始而結束，為一天中從大氣吸收 CO_2 的主要階段 (圖 3B)，此時氣孔開張，CO_2 經 PEPC 固定形成草醯乙酸 (oxaloacetic acid; OAA) 後還原為蘋果酸貯存於液胞。Phase-II 至 phase-IV 發生於光期，在 phase-II 時氣孔仍開張，PEPC 與 Rubisco 同時固定與同化 CO_2。在 phase-III 時，液胞內的蘋果酸去羧化釋出 CO_2，細胞間隙 CO_2 濃度上升，此時氣孔關閉，CO_2 與 RuBP 結合 (羧化反應) 進入卡爾文循環，此時 Rubisco 為主要催化酵素。當液胞內蘋果酸消耗殆盡，細胞間隙 CO_2 濃度降低，氣孔再度打開進入 phase-IV，此時為一天中從大氣吸收 CO_2 的次要階段 (圖 3B)。若要操作補充 CO_2，phase-I 與 phase-IV 為適合的時間點。在 phase-IV 時，PEPC 與 Rubisco 均表現其酵素活性。暗期開始後再次進入 phase-I，此時 Rubisco 停止作用 (Osmond 1978; Roberts *et al*. 1997; Guo & Lee 2006; Males & Griffiths 2017)。也有研究指出，日長大於 12 h 蝴蝶蘭 phase-IV 的固碳模式在後期轉變為 PEPC 固碳為主，此時可觀察到液胞內開始累積蘋果酸 (Hogewoning *et al*. 2021)。

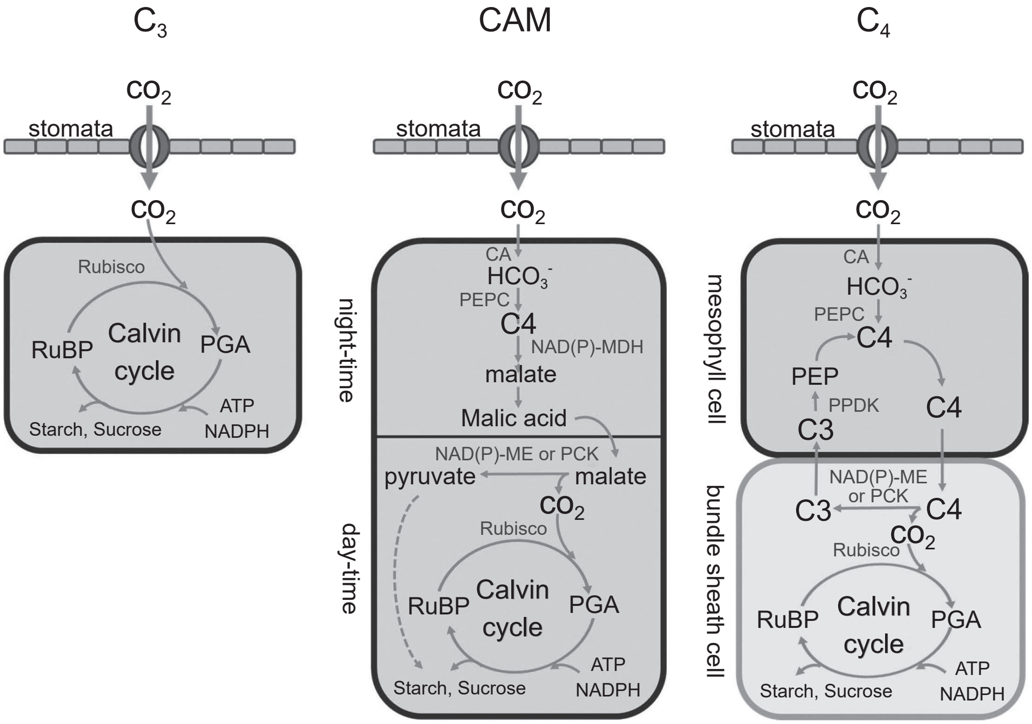

圖 2. C_3、C_4 及 CAM 植物光合作用途徑示意圖 (Adapted from Dehigaspitiya *et al*. 2019)。

Fig. 2. Schematic diagram of photosynthetic pathways in C_3, C_4, and crassulacean acid metabolism (CAM) plants (Adapted from Dehigaspitiya *et al*. 2019)

提高環境 CO_2 濃度對蝴蝶蘭光合成相關生理之影響

上述提到 phase-I 的 CO_2 總固定量，會受磷酸烯醇丙酮酸 (phosphoenolpyruvate; PEP) 的供給量與液胞的蘋果酸貯存能力所限制 (Guo & Lee 2006)。在龍舌蘭與仙人掌等 CAM 植物的研究中，短時間提高環境 CO_2 濃度雖然促進 phase-I 前期淨光合作用速率，但後期呈現補償性地降低，顯示 CO_2 吸收量提早達到飽和，但總量卻沒有改變 (Nobel & Hartsock 1986)。

已有許多研究中表明 (見表 1)，提高 CO_2 濃度能促進蝴蝶蘭淨光合作用速率、促進其 phase-I 或 phase-IV 的 CO_2 總吸收量，不論是馴化時間達 3 mo (Hogewoning *et al*. 2021)、1 wk (Ichihashi *et al*. 2008) 或僅有 2 d (Kawamitsu *et al*. 1995)。蝴蝶蘭夜間 CO_2 吸收量達飽和需要約 13 h (Ichihashi *et al*. 2008)，在足夠的夜長下也能觀察到蝴蝶蘭 phase-I 的 CO_2 飽和吸收量因為提高 CO_2 濃度而增加，顯示蝴蝶蘭 phase-I 的 CO_2 總固定量能因馴化而改變。長時間提高 CO_2 濃度可促進蝴蝶蘭葉片厚度與有機酸濃度，而較厚的葉片可能代表更多液胞貯藏蘋果酸 (Endo & Ikushima 1997; Xu *et al*. 2019)，顯示提高 CO_2 濃度能增進蝴蝶蘭光合作用能力與蘋果酸貯藏能力。

落地生根 (*Kalanchoe pinnata*) 之研究顯示，夜間大氣 CO_2 濃度已接近其光合作用 CO_2 飽和點，日間 CO_2 飽和點則高於大氣濃度 (Winter & Engelbrecht 1994)，而關於蝴蝶蘭光合作用之 CO_2 飽和點未有一致性的結論。根據 Kawamitsu *et al*. (1995) 的研究，當日/夜溫 25/20℃，光照充足下應介於 700–1,400 μL L^{-1} CO_2 之間；而在 Ichihashi *et al*. (2008) 的研究中，phase-I 之 CO_2 吸收速率在 1,200 μL L^{-1} CO_2 下仍未達飽和，並且在 CO_2 濃度 1,500 μL L^{-1} 下，phase-I 的 CO_2 飽和吸收量仍高於 1,000 μL L^{-1} 下約 30%，而 phase-IV 之 CO_2 吸收速率

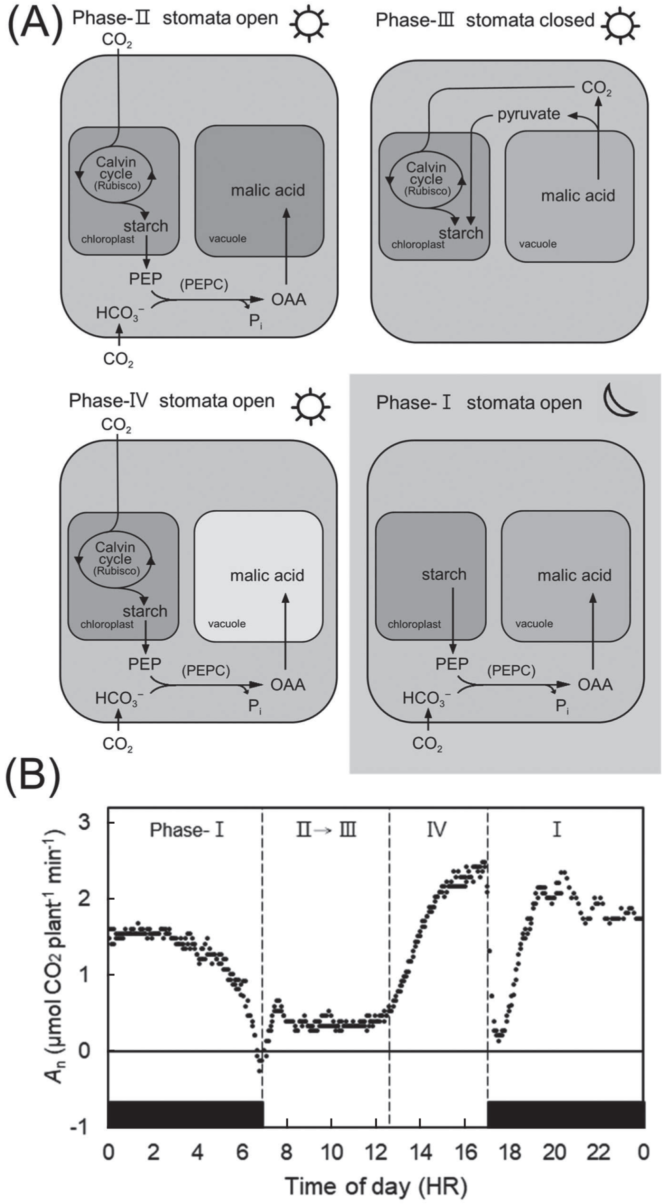

圖 3. (A) 蝴蝶蘭光合作用碳代謝途徑與 (B) 其植株 CO_2 吸收量日變化。

Fig. 3. (A) Carbon metabolism pathway in photosynthesis of *Phalaenopsis* and (B) diurnal variation of plant carbon dioxide (CO_2) uptake.

在 25℃、300 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD) 下，CO_2 濃度達 1,800 μL L^{-1} 仍未有飽和的趨勢，整體來說蝴蝶蘭之日間與夜間 CO_2 飽和點均高於 700 μL L^{-1}。關於蝴蝶蘭光合作用之 CO_2 補償點，目前研究中亦沒有明確數值，但從其他 CAM 植物 (如落地生根) 研究顯示，日間光合作用之 CO_2 補償點高於 100 μL L^{-1}，而夜間則低於 30 μL L^{-1} (Winter & Engelbrecht 1994)。

無論 C_3 或 CAM 植物，環境 CO_2 濃度提高能使氣孔導度或氣孔密度下降，而淨光合作用速率仍維持或提高，因此能使光合作用

表 1. 二氧化碳添加濃度對蝴蝶蘭光合作用影響相關試驗結果整理。

Table 1. Summary of experimental results on the effects of elevated carbon dioxide (CO_2) concentrations on the photosynthesis of *Phalaenopsis*.

Test variety (*Phalaenopsis*)	CO_2 elevated concentration (μL L^{-1})	CO_2 enrichment period	CO_2 enrichment time	Gas exchange measured condition	Result	Reference
P. Casablanca Moo × *P. Buera* Flora	350 (CK), 700, 1,400, 2,800	2 wk in vegetative (V) stage	Whole day	Greenhouse; 25/20℃, 5,000, 15,000, 30,000, 45,000 Lux × 11 h	CO_2 uptake in phase-I saturated between 700–1,400 μL L^{-1} CO_2 at optimal light intensity (15,000, 30,000 lux), CO_2 enrichment enhanced malic acid content in leaves and phosphoenolpyruvate carboxylase (PEPC) enzyme activity during phase-I.	Kawamitsu *et al*. 1995
'70', 'L'	380 (CK), 950	1 wk in V stage	Whole day	Greenhouse; 25/20℃, 180 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD)	CO_2 uptake in phase-I increased by 82%.	Lootens & Heursel 1998
White Dream 'MM74', 'Miki', 'Cinderella Beauty'	500 (CK), 1,000, 1,500	1 wk in V stage	Not specified	Growth chamber; 20℃, 400 μmol m^{-2} s^{-1} PPFD	Promoted CO_2 uptake in phase-I and phase-IV.	Ichihashi *et al*. 2008
	Various concentrations	1 wk in V stage	Not specified	Growth chamber; 25℃	The A_n in phase-I did not saturate at 1,200 μL L^{-1} CO_2, and the A_n in phase-IV did not saturate under 300 μmol m^{-2} s^{-1} PPFD and 1,800 μL L^{-1} CO_2.	
Queen Bear 'Mentefon'	450 (CK), 800, 1,600	12–36 wk in V stage	Last 6 h of the dark period	Growth chamber; 29℃ , 50% RH, 160 μmol m^{-2} s^{-1} PPFD × 12 h	g_s, A_n, and CO_2 uptake in day-time increased with higher [CO_2] across phases, transpiration rate and night-time water use efficiency increased.	Yun *et al*. 2018
Queen Bear 'Mentefon'	400 (CK), 800, 1,200	Reproductive (R) stage, 16 wk after the starting of flower induction	00:00–06:00	Growth chamber; 23/18℃, 50–55% RH, 90 (low light) or 260 (high light) μmol m^{-2} s^{-1} PPFD × 12 h	Under low light, 800 μL L^{-1} CO_2 or under high light, 1,200 μL L^{-1} CO_2 promoted A_n of phase-I, the impact on g_s or water use efficiency was not significant.	Cho *et al*. 2019
'Neyshan Guniang'	400 (CK), 800	30 or 120 d in V stage	18:00–06:00	Greenhouse; 28/26℃, 85% RH, 50% shading	The stomatal conductance (g_s) in phase-I decreased by approximately 30%, net photosynthesis rate (A_n) increased by 46–50%, soluble protein content decreased, Rubisco and PEPC enzyme activities enhanced.	Xu *et al*. 2019
'Sacramento'	400 (CK), 800	12–16 wk in V stage, 25–29 wk in R stage	Not specified	Growth chamber; 4 d acclimation for elevated CO_2 or not, 70% RH, 15 h photoperiod, 28.5℃ and daily light integral (DLI) 6.4 mol m^{-2} d^{-1} in V stage, 19.5℃ and DLI 8.3 mol m^{-2} d^{-1} in R stage	The g_s decreased by approximately 30%. CO_2 uptake in phase-I increased by 29% and 31% during V and R stages, respectively, while phase-IV increased by 21% and 45%, respectively. Acclimation did not affect the promotion level of CO_2 uptake by CO_2 enrichment.	Hogewoning *et al*. 2021

的水分利用效率增加 (Brodribb *et al*. 2009)。蜻蜓鳳梨屬 (*Aechmea*) CAM 植物長時間暴露在 700 μL L^{-1} CO_2 下，phase-I 之氣孔導度下降達 50%，但 CO_2 吸收量不變 (Ceusters *et al*. 2008)。蝴蝶蘭則無論是長時間 (連續 3 mo 以上) 或短時間暴露於 800 μL L^{-1} CO_2 下，使 phase-I (或單日最高氣孔導度) 降低約 30%，但 phase-I 之淨光合作用速率仍增加約 40% 或增加 30%CO_2 總吸收量 (Xu *et al*. 2019)，而 phase-IV 之總吸收 CO_2 量在營養生長與開花時也分別增加 21% 與 45% (Hogewoning *et al*. 2021)。然環境中 CO_2 濃度過高可能使植物氣孔關閉，在光合作用 CO_2 飽和點以內，也並非施用越高濃度 CO_2 就能達到最佳效益。但是，也有些研究指出在提高 CO_2 濃度環境下，蝴蝶蘭氣孔導度不受影響或甚至提高 (Yun *et al*. 2018; Cho *et al*. 2019)，而無論氣孔導度反應如何，目前報告顯示 CO_2 補充濃度在 1,600 μL L^{-1} 內，均對蝴蝶蘭淨光合作用速率有不同程度的促進作用 (見表 1)。

提高環境 CO_2 濃度下蝴蝶蘭生長與開花之表現

栽培環境長期補充 CO_2 濃度達 700–800 μL L^{-1}，使蝴蝶蘭葉片增厚，葉面積、植株乾鮮重、葉片中澱粉含量、可溶性糖含量、葉綠素濃度及有機酸濃度均增加 (Endo & Ikushima 1997; Kataoka *et al*. 2004; Xu *et al*. 2019)。在龍舌蘭與仙人掌等其他 CAM 植物研究也顯示，在 650 μL L^{-1} CO_2 下能促進其植株整體生長量 (Nobel & Hartsock 1986)。提高 CO_2 濃度使蝴蝶蘭的根冠比增加 (Xu *et al*. 2019)，在部分研究中促進生物量的結果也在根部較顯著 (Kromwijk *et al*. 2014; Kim *et al*. 2017)。

在花朵性狀表現方面，多數研究結果均顯示補充 CO_2 的正面效果 (見表 2)，包含提早開花 (Cho *et al*. 2019)，促進花梗數、花朵數、側枝數量或花梗長度 (Endo & Ikushima 1997; Kromwijk *et al*. 2014; Cho *et al*. 2020)，促進花梗乾重 (Kromwijk *et al*. 2014)、鮮重、可溶性醣類及蘋果酸等有機酸濃度，並使切花瓶插壽命較長 (Endo & Ikushima 1997)。

然不同發育階段補充 CO_2 的影響不同，若要增進蝴蝶蘭花梗與花芽的數量，在催花後之生殖生長時期補充 CO_2 之影響可能較為關鍵。在 Kromwijk *et al*. (2014) 的研究中，催花前全天施予 1,000 μL L^{-1} CO_2 30 wk 後，能促進葉面積與根部生長量，但僅在此營養生長期補充 CO_2，雖然增加生長量，但沒有提升花芽數與花梗數等性狀；而在開始催花 (日/夜溫 19/18℃) 後整日施予 1,000 μL L^{-1} CO_2 30 wk 後，無論催花前有沒有補充 CO_2，花芽數與多梗數植株比例均有增加。

不同研究中顯示 (見表 2)，補充 CO_2 濃度在 1,200 μL L^{-1} 內對蝴蝶蘭開花品質多有效益，催花開始後於夜間施予 800 μL L^{-1} CO_2，使 Queen Bear ‘Mentefon’ 開花所需時間從 19 wk 減少至 16 wk，並促進其花梗長度，使花苞數量增加 20% 以上，當補充 CO_2 至 1,200 μL L^{-1} 時花梗分叉數量顯著增加，但補充 CO_2 則使花朵較小 (Cho *et al*. 2019, 2020)。從營養生長至開花期間 (共約 30 mo) 於夜間補充至 1,000 μL L^{-1} CO_2，使蝴蝶蘭 ‘Yukimai’ 花梗數、開花數及花梗鮮重分別增加 29%、42% 及 58%，花梗可溶性醣類與蘋果酸等有機酸濃度提高，切花壽命從 62 d 增加至 80 d (Endo & Ikushima 1997)。

然而在部分研究中，CO_2 補充濃度在 800 μL L^{-1} 以上時對蝴蝶蘭生育造成負面影響。夜間施予蝴蝶蘭 Queen Bear ‘Mentefon’ 800 μL L^{-1} 之 CO_2，雖然促進其淨光合作用速率與新葉發育，使葉片較多，但沒有增加生物量，甚至當濃度補充至 1,600 μL L^{-1} 時，地上部鮮重與乾重反而減少 (Yun *et al*. 2018)。蝴蝶蘭 ‘Fuller’s Pink Swallow’ 從催花前營養生長時期到花梗發育期間，連續於夜間補充 CO_2 至 800 μL L^{-1}，造成開花延遲、花梗鮮重減少，甚至補充至 1,600 μL L^{-1} 時加劇花苞萎凋 (withering) 掉落，此結果可能是因為葉芽積貯強度過高，競爭花芽發育亦或栽培管理不當所致 (Kim *et al*. 2017)。

CO_2 添加效益之限制因子

長時間提高 CO_2 濃度處理對植物光合作用促進的程度不一定能維持等量的效益，這部

表 2. 二氧化碳濃度對蝴蝶蘭生長與開花之影響相關試驗結果整理。

Table 2. Summary of experimental results on the effects of elevated carbon dioxide (CO_2) concentrations on the growth and flowering of *Phalaenopsis*.

Test variety (*Phalaenopsis*)	CO_2 elevated concentration ($\mu L\ L^{-1}$)	CO_2 enrichment period	CO_2 enrichment time	Experimental condition	Result	Reference
'Yukimai'	438 (CK), 700, 1,000	From V stage to flowering	Sunset to sunrise	Greenhouse; 20–30℃, 5,000–7,000 lux	Under 700 and 1,000 $\mu L\ L^{-1}$ CO_2, the increase of spike number was 11% and 29%, the flower numbers were 10% and 42%, the spike fresh weight was 13% and 58%, and the vase life of cut flower increased from 62 d to 66 and 80 d, respectively.	Endo & Ikushima 1997
White Dream × *P*. Yukimai Dream	640 (CK), 1,000–3,000	R stage, 4 wk after the starting of flower induction	Not specified	Growth chamber; 20℃, 135 $\mu mol\ m^{-2}\ s^{-1}$ photosynthetic photon flux density (PPFD)	A significant increase in leaf sucrose accumulation after 2–3 wk of treatment, which reduced the days required for spike emergence from 43.3 to 33.4, but there were no differences in days to flowering, flower number, or flower size.	Kataoka *et al*. 2004
'Brussels', 'Pink Twilight', 'Sacramento', 'White Moon'	433 (CK), 1,000	V stage, 30 wk before flower induction	Whole day	Growth chamber; 28/28℃, 70% RH, 72–90 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h	Increased leaf area and root dry weight by 17%. There were no significant differences in leaf number, vegetative growth after flowering, flower bud number, spike number, or spike dry weight.	Kromwijk *et al*. 2014
	433–440 (CK), 1,000	R stage, 18 wk after the starting of flower induction	Whole day	Growth chamber; 20.0/18.5℃, 70% RH, 139 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h	Increased spike numbers by 9%, proportion of multi-spike plants increased from 66% to 81%.	
	433–440 (CK), 1,000	From V stage to flowering, 30 wk before and 18 wk after the starting of flower induction	Whole day	Growth chamber; 70% RH; 28/28℃ and 72–90 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h before flowering induction; 20/18.5℃ and 139 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h after flowering induction	The root dry weight increased by 20%, spike numbers increased by 11%, proportion of multi-spike plants increased from 66% to 80%, and spike dry weight increased by 26%.	
'Fuller's Pink Swallow'	450 (CK), 800, 1,600, 2,400	From V stage to flowering, 31 wk before flowering	Last 6 h of the dark period	Growth chamber, 50% RH; 29/29, 23/18, 25/20℃ and 120, 160, 160 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h in V stage, flowering induction, spike development periods, respectively	Root biomass increased; length of flower spike branch increased with higher [CO_2]. Days to flowering increased from 170 to 203 d, flower numbers decreased by 40% (3.6 fewer flowers), and spike weights decreased by more than 30% with 800 $\mu L\ L^{-1}$ CO_2. When [CO_2] were above 1,600 $\mu L\ L^{-1}$, leaf numbers increased by approximately 2, the leaf became larger, flower bud numbers increased but dropped severely.	Kim *et al*. 2017

表 2. 二氧化碳濃度對蝴蝶蘭生長與開花之影響相關試驗結果整理。(續)

Table 2. Summary of experimental results on the effects of elevated carbon dioxide (CO_2) concentrations on the growth and flowering of *Phalaenopsis*. (continued)

Test variety (*Phalaenopsis*)	CO_2 elevated concentration ($\mu L\ L^{-1}$)	CO_2 enrichment period	CO_2 enrichment time	Experimental condition	Result	Reference
Queen Bear 'Mentefon'	450 (CK), 800, 1,600	12–36 wk in V stage	Last 6 h of the dark period	Growth chamber; 29℃, 50% RH, 160 $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h	Increased the rate of leaf development and leaf numbers, the fresh and dry weight did not increase after 36-wk treatment. When rising [CO_2] to 1,600 $\mu L\ L^{-1}$, the fresh and dry weight of shoot decreased.	Yun *et al*. 2018
Queen Bear 'Mentefon'	400 (CK), 800, 1,200	R stage, 16 wk after the starting of flower induction	00:00–06:00	Growth chamber, 23/18℃, 50–55% RH, 90 (low light) or 260 (high light) $\mu mol\ m^{-2}\ s^{-1}$ PPFD × 12 h	The time to flowering reduced by approximately 40% under 800 and 1,200 $\mu L\ L^{-1}$ CO_2. The number of spike branches increased at 1,200 $\mu L\ L^{-1}$ CO_2.	Cho *et al*. 2019
'Neyshan Guniang'	400 (CK), 800	30 or 120 d in V stage	18:00–06:00	Greenhouse; 28/26℃, 85% RH, 50% shading	Increased starch, soluble sugar, and titratable acid contents per leaf area, soluble protein content decreased. In the 120 d treatment, plant dry weight, fresh weight, leaf area, leaf thickness, and root-shoot ratio increased.	Xu *et al*. 2019
Queen Bear 'Mentefon'	400 (CK), 800	R stage, 17 wk after the starting of flower induction	00:00–06:00	Greenhouse; 51%–76% RH; 24.5/20.5℃ in flowering induction periods, 25.1–27.7/20.8–24.0℃ in spike development periods; daily light integral (DLI) gradually increased from 4.6 to 10.1 $mol\ m^{-2}\ d^{-1}$ through the treatment	The spike length and flower bud numbers increased, time to flowering was shortened, but flower diameter reduced.	Cho *et al*. 2020

分可能與馴化結果有關 (Moore *et al*. 2002)。在以 C_3 植物為主的研究中，部分植物長時間暴露在較高 CO_2 濃度時會減少氮元素投入光合作用系統，使在較低的 Rubisco 含量下，維持與大氣 CO_2 濃度下近似的淨光合作用速率 (Sage 1994; Moore *et al*. 2002; Wolfe *et al*. 2002)。蝴蝶蘭在長期 (夜間) 提高 CO_2 濃度下，也觀察到葉片單位面積可溶性蛋白質含量減少，Rubisco 與 PEPC 之酵素活性提升，不過淨光合作用速率仍有增加，增加的程度隨著暴露時間增長僅有些微降低；例如蝴蝶蘭 'Neyshan Guniang' 在 800 μL L^{-1} CO_2 下 30 d 後，phase-I 之淨光合作用速率提升 50%，而 120 d 後仍有提升 40% 以上 (Xu *et al*. 2019)，顯示長期補充 CO_2 對光合作用促進的程度可能會隨暴露時間增長而變小，但仍有顯著效益。其他會限制 CO_2 補充效益的因素，包含供源-積儲 (source-sink) 間失衡，光合作用能力提升但積儲的強度不足以利用過多的碳水化合物，對光合作用造成回饋抑制 (Bunce & Sicher 2003; Qian *et al*. 2012)；甚至栽培容器的空間限制根部生長，也會降低補充 CO_2 對光合作用的效益 (Arp 1991)。由此可知，提升光合作用不一定會完全反應在生長量的增加，必須要有其他生長條件相配合。

栽培管理之調整

氮肥補充

補充 CO_2 的效益要反應在生長量，需有適當的環境與充足的營養條件。部分植物在長時間提高 CO_2 下會減少葉片中的 Rubisco 含量，使其與大氣 CO_2 濃度下淨光合作用速率無顯著差異 (Sage 1994; Moore *et al*. 2002)。長期提高 CO_2 濃度降低蝴蝶蘭葉片可溶性蛋白質含量，而增加氮肥施用可減少此降低程度。雖然增加氮肥施用沒有改變補充 CO_2 濃度後淨光合作用速率的提升幅度，但能使葉片厚度與植株鮮重、乾重增加，顯示在補充 CO_2 的情況下，提供充足的氮肥有助於實現更高的植株生長量 (Xu *et al*. 2019)。

CO_2 補充時機

提高 CO_2 濃度能促進光合作用速率，但促進效果會因為過多碳水化合物造成回饋抑制而降低。回饋抑制容易發生於積儲強度較弱時，例如較少的果實數量 (Qian *et al*. 2012) 或營養器官膨大之前。此外，環境也會造成影響，例如甘藍在晴天時累積較多光合產物，隔日則容易發生回饋抑制 (Bunce & Sicher 2003)，因此在栽培策略上應考量植株不同發育階段所需之光合產物量。蝴蝶蘭生產常以 20℃進行催花，利用涼溫促進其花芽分化，在此營養生長轉換為生殖生長的過程中，可觀察到葉片中可溶性醣類累積 (Kataoka *et al*. 2004)，此時可能為補充 CO_2 更有效益的發育階段。低溫下提高 CO_2 濃度，促進蝴蝶蘭光合作用的結果將更顯著。在 25℃與 1,200 μL L^{-1} CO_2 條件下，蝴蝶蘭 White Dream 'MM74' phase-I 淨光合作用速率介於 7–8 μmol CO_2 m^{-2} s^{-1}，而溫度降低至 20℃時為 17–18 μmol CO_2 m^{-2} s^{-1} (Ichihashi *et al*. 2008)。在 20℃催花時施予 *P*. White Dream × *P*. Yukimai Dream 1,000 μL L^{-1} 以上之 CO_2，2–3 wk 後葉片中蔗糖之累積量顯著增加，而葉片中可溶性醣類含量越高則花芽創始 (initiation) 越快，抽梗所需日數從 43.3 d 減少為 33.4 d，但未影響到花日數 (Kataoka *et al*. 2004)。

結語

本文綜合討論提高環境 CO_2 濃度對蝴蝶蘭光合作用與生長發育之影響，適當栽培條件下提高 CO_2 濃度能促進蝴蝶蘭光合作用速率、植株生長量及開花品質，補充 CO_2 時也須注意氮肥等礦物營養供應是否充足，以及高濃度 CO_2 可能造成之傷害。溫度、光照及礦物營養均會影響 CO_2 的補充效益，補充效果也可能因品種而異。而現今的栽培與環控條件不同以往，類似的試驗可能得到不同結果，未來宜進一步研究探討 CO_2 補充相關議題，並針對不同環境條件與發育階段精準管理，以提升蝴蝶蘭的生產效率。

引用文獻

Arp, W. J. 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO_2. Plant Cell Environ. 14:869–875. doi:10.1111/j.1365-3040.1991.tb01450.x

Bowes, G. 1991. Growth at elevated CO_2: Photosynthetic responses mediated through rubisco. Plant Cell Environ. 14:795–806. doi:10.1111/j.1365-3040.1991.tb01443.x

Brodribb, T. J., S. A. M. McAdam, G. J. Jordan, and T. S. Feild. 2009. Evolution of stomatal responsiveness to CO_2 and optimization of water-use efficiency among land plants. New Phytol. 183:839–847. doi:10.1111/j.1469-8137.2009.02844.x

Bunce, J. A. and R. C. Sicher. 2003. Daily irradiance and feedback inhibition of photosynthesis at elevated carbon dioxide concentration in *Brassica Oleracea*. Photosynthetica 41:481–488. doi:10.1023/B:PHOT.0000027511.44995.66

Ceusters, J., A. M. Borland, E. Londers, V. Verdoodt, C. Godts, and M. P. De Proft. 2008. Diel shifts in carboxylation pathway and metabolite dynamics in the CAM *Bromeliad Aechmea* 'Maya' in response to elevated CO_2. Ann. Bot. 102:389–397. doi:10.1093/aob/mcn105

Cho, A. R., S. W. Chung, and Y. J. Kim. 2020. Flowering responses under elevated CO_2 and graded nutrient supply in *Phalaenopsis* Queen Beer 'Mantefon'. Sci. Hortic. 273:109602. doi:10.1016/j.scienta.2020.109602

Cho, A. R., S. J. Song, S. W. Chung, and Y. J. Kim. 2019. CO_2 enrichment with higher light level improves flowering quality of *Phalaenopsis* Queen Beer 'Mantefon'. Sci. Hortic. 247:356–361. doi:10.1016/j.scienta.2018.12.030

Dehigaspitiya, P., P. Milham, G. J. Ash, K. Arun-Chinnappa, D. Gamage, A. Martin, ... S. Seneweera. 2019. Exploring natural variation of photosynthesis in a site-specific manner: Evolution, progress, and prospects. Planta 250:1033–1050. doi:10.1007/s00425-019-03223-1

Endo, M. and I. Ikushima. 1997. Effects of CO_2 enrichment on yields and preservability of cut flowers in *Phalaenopsis*. J. Japan. Soc. Hort. Sci. 66:169–174. doi:10.2503/jjshs.66.169

Guo, W. J. and N. Lee. 2006. Effect of leaf and plant age, and day/night temperature on net CO_2 uptake in *Phalaenopsis amabilis* var. Formosa. J. Amer. Soc. Hortic. Sci. 131:320–326. doi:10.21273/JASHS.131.3.320

Hogewoning, S. W., S. A. J. Van Den Boogaart, E. Van tongerlo, and G. Trouwborst. 2021. CAM-physiology and carbon gain of the orchid *Phalaenopsis* in response to light intensity, light integral and CO_2. Plant Cell Environ. 44:762–774. doi:10.1111/pce.13960

Hung, T. C. 2012. Meta analysis of photosynthetic pathway in *Phalaenopsis* aphrodite combining physiological approach and gene expression profiling studies. Master Thesis. Department of Horticulture and Landscape Architecture, National Taiwan University. Taipei, Taiwan. 157 pp. (in Chinese with English abstract)

Ichihashi, S., T. Higuchi, H. Shibayama, Y. Tesima, Y. Nishiwaki, and K. Ota. 2008. Aspects of CO_2 uptake in the crassulacean acid metabolism orchid *Phalaenopsis*. Acta Hortic. 766:245–256. doi:10.17660/ActaHortic.2008.766.33

Kataoka, K., K. Sumitomo, T. Fudano, and K. Kawase. 2004. Changes in sugar content of *Phalaenopsis* leaves before floral transition. Sci. Hortic. 102:121–132. doi:10.1016/j.scienta.2003.12.006

Kawamitsu, Y., M. Naka, H. Nakayama, and F. Sekizuka. 1995. Effects of elevated CO_2 on crassulacean acid metabolism in *Phalaenopsis*. Bull. Dept. Agric. Ryukyu Univ. 42:23–32.

Kim, H. J., A. R. Cho, K. S. Park, and Y. J. Kim. 2017. Effect of CO_2 enrichment on growth and flowering of *Phalaenopsis*. Hort. J. 86:389–394. doi:10.2503/hortj.OKD-027

Kromwijk, J. A. M., E. Meinen, and T. A. Dueck. 2014. The effect of elevated CO_2 on the vegetative and generative growth of *Phalaenopsis*. Acta Hortic. 1025:155–161. doi:10.17660/ActaHortic.2014.1025.23

Lootens, P. and J. Heursel. 1998. Irradiance, temperature, and carbon dioxide enrichment affect photosynthesis in *Phalaenopsis* hybrids. HortScience 33:1183–1185. doi:10.21273/HORTSCI.33.7.1183

Makino, A. and T. Mae. 1999. Photosynthesis and plant growth at elevated levels of CO_2. Plant Cell Physiol. 40:999–1006. doi: org/10.1093/oxfordjournals.pcp.a029493.

Males, J. and H. Griffiths. 2017. Stomatal biology of CAM plants. Plant Physiol. 174:550–560. doi:10.1104/pp.17.00114

Moore, B. D, S. H. Cheng, D. Sims, and J. R. Seemann. 2002. The biochemical and molecular basis for acclimation to elevated CO_2. Plant Cell Environ. 22:567–582. doi:10.1046/j.1365-3040.1999.00432.x

Nobel, P. S. and T. L. Hartsock. 1986. Short-term and long-term responses of crassulacean acid metabolism plants to elevated CO_2. Plant Physiol. 82:604–

606. doi:10.1104/pp.82.2.604

Osmond, C. B. 1978. Crassulacean acid metabolism: A curiosity in context. Annu. Rev. Plant Biol. 29:379–414. doi:10.1146/annurev.pp.29.060178.002115

Qian, T., J. A. Dieleman, A. Elings, and L. F. M. Marcelis. 2012. Leaf photosynthetic and morphological responses to elevated CO_2 concentration and altered fruit number in the semi-closed greenhouse. Sci. Hortic. 145:1–9. doi:10.1016/j.scienta.2012.07.015

Roberts, A., A. M. Borland, and H. Griffiths. 1997. Discrimination processes and shifts in carboxylation during the phases of crassulacean acid metabolism. Plant Physiol. 113:1283–1292. doi:10.1104/pp.113.4.1283

Sage, R. F. 1994. Acclimation of photosynthesis to increasing atmospheric CO_2: The gas exchange perspective. Photosynth. Res. 39:351–368. doi:10.1007/BF00014591

Winter, K. and B. Engelbrecht. 1994. Short-term CO_2 responses of light and dark CO_2 fixation in the crassulacean acid metabolism plant *Kalanchoë pinnata*. J. Plant Physiol. 144:462–467. doi:10.1016/S0176-1617(11)82123-1

Wolfe, D., R. Gifford, D. Hilbert, and Y. Luo. 2002. Integration of photosynthetic acclimation to CO_2 at the whole-plant level. Glob. Change Biol. 4:879–893. doi:10.1046/j.1365-2486.1998.00183.x

Xu, S. P., X. Y. Yuan, Y. Zhang, and Q. S. Ye. 2019. Effect of elevated CO_2 combined with two nitrogen levels on photosynthesis, growth and leaf structure in CAM orchid *Phalaenopsis*. Intl. J. Agric. Biol. 22:882–890.

Yun, D. L., H. J. Kim, and Y. J. Kim. 2018. CO_2 enrichment increased leaf initiation and photosynthesis in Doritaenopsis Queen Beer ‘Mantefon’ orchids. Hortic. Environ. Biotechnol. 59:159–165. doi:10.1007/s13580-018-0025-z

Effects of Carbon Dioxide Enrichment on Photosynthesis, Growth, and Flowering of *Phalaenopsis*

Ming-Hsuan Tsai[1,*] and Wei-Ling Chen[2]

Abstract

Tsai, M. H. and W. L. Chen. 2025. Effects of carbon dioxide enrichment on photosynthesis, growth, and flowering of *Phalaenopsis*. J. Taiwan Agric. Res. 74(2):129–140.

The production of *Phalaenopsis* is equipment- and energy-intensive. To improve production and energy efficiency, carbon dioxide (CO_2) enrichment is worthy of evaluation and investment. This article reviews relevant research on the application of CO_2 enrichment in *Phalaenopsis* cultivation. The *Phalaenopsis* growth rates or biomass can be promoted during the vegetative stage by increasing CO_2 concentrations to 700–800 $\mu L\ L^{-1}$, while insufficient nitrogen fertilizer may limit the benefits. Enrich CO_2 to 1,000 $\mu L\ L^{-1}$ during the reproductive stage could shorten the days to spike emergence and enhance the numbers of flower spikes and buds, spike weight, and vase life. However, some studies reported that the concentration of CO_2 went up to 1,600 $\mu L\ L^{-1}$ may lead to decreases in shoot fresh and dry weights or flower bud drop.

Key words: Carbon dioxide enrichment, Crassulacean acid metabolism, Growth stage, Greenhouse.

Received: December 5, 2024; Accepted: February 11, 2025.
[*] Corresponding author, e-mail: krill1318@gmail.com
[1] Assistant Research Fellow, Department of Industrial Application, Floriculture Experiment Branch, Taiwan Agricultural Research Institute, Yunlin County, Taiwan, ROC.
[2] Associate Research Fellow and Division Director, Department of Industrial Application, Floriculture Experiment Branch, Taiwan Agricultural Research Institute, Yunlin County, Taiwan, ROC.

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):141–150 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0004

探討植物揮發性有機化合物的生物性功能

何佳勳[1,*] 楊滿霞[2] 蕭巧玲[2] 侯雅玲[1]

摘要

何佳勳、楊滿霞、蕭巧玲、侯雅玲。2025。探討植物揮發性氣體的生物性功能。台灣農業研究 74(2):141–150。

植物釋放的揮發性有機化合物 (plant volatile organic compounds; pVOCs) 在生態體系中具有不同的生物性功能，如啟動植物防禦機制、植物間訊號傳遞、協助授粉與種子傳播、促進作物生長與適應環境逆境及提高農產品品質等。當植物遭受植食性害蟲攻擊時，會誘導釋放特殊的揮發性物質 (herbivore-induced plant volatiles; HIPVs)，吸引害蟲的天敵並啟動鄰近植物的防禦反應。此外，pVOCs 還可透過植物間訊號傳遞機制，提升鄰近植株對逆境的抵抗能力。pVOCs 的生合成來自多種生化途徑，且可分成四大類包含萜類化合物 (terpenoids)、苯丙烷類/苯類 (phenylpropanoids/benzenoids) 化合物、脂肪酸 (fatty acid) 及胺基酸 (amino acid) 衍生物。另一方面，環境因子會影響 pVOCs 的釋放量、成分含量及化學組成，其中又以溫度為關鍵因素。pVOCs 可作為生物防治與有機農業應用的潛在工具，惟其易揮發性、高生物降解性、環境干擾穩定性及生產成本高等問題，導致在農業上的應用仍受限制。若要擴大 pVOCs 的應用，仍需進一步研究與技術優化，以期能克服限制並取代傳統農藥，進而提升農業永續性。

關鍵詞：揮發性有機化合物、生物性功能、萜類化合物、生合成、溫度。

前言

植物所釋放的揮發性有機化合物 (plant volatile organic compounds; pVOCs) 在生態體系中扮演重要的訊息傳遞角色，其會吸引授粉媒介昆蟲協助花粉傳播、果實釋放香氣吸引動物協助種子散布以及植物地上部與地下部所釋放的特殊氣味，可防禦植食性動物 (herbivore) 與病原體等 (Raguso 2008; Unsicker *et al*. 2009; Ali *et al*. 2012; Hiltpold & Turlings 2012; Dudareva *et al*. 2013)。此外，pVOCs 還可保護植物避免遭受生物性 (biotic) 與非生物性 (abiotic) 逆境的損害，尤其當植物面對植食性害蟲攻擊時，則會誘導植物釋放揮發性物質 (herbivore-induced plant volatiles; HIPVs) 以吸引植食性害蟲的天敵，並引發鄰近植物的防禦反應，藉此降低植物的損害 (James & Grasswitz 2005; Ali *et al*. 2012)。另一方面，當植物遭受機械性損傷時也會短時間誘發植物釋放簡單的 pVOCs (Giorgi *et al*. 2015)。已知 pVOCs 對植物的防禦作用與授粉繁殖屬於物種特異性，主要取決於植物的遺傳特性，一般植物釋放 pVOCs 的組織器官，主要有來自開花植物的花與營養組織、針葉樹的葉子與莖，以及草本植物 (如薄荷與羅勒) 的葉片等，均會釋放出揮發性氣體 (McConkey *et al*. 2000; Knudsen *et al*. 2006; Vassão *et al*. 2006)，且不同器官在面對相同的生物性與非生物性逆境所釋放的 pVOCs 反應也不盡相同。本文旨在綜整植物揮發性有機化合物於生物性功能上的研究進展，探討其防禦機制、訊號傳遞、生合成途徑及應用潛力，並評估其在永續農業中作為生物防治資材或有機農業應用之潛力與限制，以期作為後續研究與應用技術開發之參考依據。

投稿日期：2025 年 2 月 21 日；接受日期：2025 年 4 月 7 日。
* 通訊作者：chia0423@tari.gov.tw
[1] 農業部農業試驗所作物組助理研究員。臺灣 臺中市。
[2] 農業部農業試驗所作物組副研究員。臺灣 臺中市。

植物揮發性成分的生物性功能

植物防禦機制 (plant defense mechanisms)

植物所釋放的 pVOCs 可作為植食性動物篩選寄主植物的重要訊息，其主要貯存在特異化組織，如樹脂管或腺毛 (Mita *et al*. 2002)，且 pVOCs 也具有防禦機制功能，可降低植食性動物的攝食活力，並能抑制病原菌的蛋白酶活性 (Baier *et al*. 2002; Niinemets *et al*. 2013; Brilli *et al*. 2019)。植物防禦機制可分為直接與間接 2 種，其中直接防禦 (direct defense) 即植物可釋放毒性或驅避性的 pVOCs 以抑制害蟲或病原體；而間接防禦 (indirect defense) 則是植物遭受攻擊時會釋放 pVOCs 以吸引植食性害蟲的天敵 (Gols 2014)。Neri *et al*. (2007) 報告指出檸檬醛 (citral)、香芹酚 (carvacrol) 及反式-2-己烯醛 (*trans*-2-hexenal) 能有效阻礙核果褐腐病菌 (*Monilinia laxa*) 體外生長與孢子萌發。Morse *et al*. (2012) 研究指出栽培在溫室中的番茄 (*Lycopersicon esculentum* Mill) 花朵會釋放 β-phellandrene、2-carene、α-pinene 及 p-cymene 等 4 種單萜類揮發物，這些 pVOCs 可能具備毒性或驅避作用，導致熊蜂 (*Bombus impatiens* Cresson) 對其釋放量較高的花朵產生排斥反應。Marques *et al*. (2014) 研究顯示柑橘 (*Citrus sinensis* var. Valência) 花朵中所產生的芳樟醇 (linalool) 對炭疽病菌 (*Colletotrichum acutatum*) 具有明顯的體外抑制作用，當芳樟醇濃度達 1,000 mg mL^{-1} 時，則能完全抑制菌絲生長。此外，α-pinene、limonene 及 3-carene 等成分也具有抗真菌與抑制害蟲及線蟲等活性 (Hollingsworth 2005; Xu *et al*. 2014; Hwang *et al*. 2021)，綜合上述研究均屬植物直接防禦機制。Cheng *et al*. (2007) 利用轉基因水稻大量表達 OsTPS3 以產生較多的 (E)-β-caryophyllene，此揮發性成分可吸引寄生蜂 (*Anagrus nilaparvatae*) 保護水稻植株免受植食性昆蟲的侵害，進而提升水稻地上部的間接防禦能力。

植物間訊號傳遞 (plant-plant communication)

pVOCs 可作為植物與植物之間內部及外部的訊息傳遞物質，當植物遭受威脅時會釋放 pVOCs 作為訊息傳導以誘導系統性反應，使周圍植物提前啟動防禦機制，進而提升鄰近植物對抗逆境的抵抗力 (Heil & Bueno 2007; Ninkovic *et al*. 2021)，其中異戊二烯 (isoprene)、甲醇 (methanol) 及植物激素乙烯 (ethylene) 等具有高度揮發性，其訊息傳遞僅限於較短距離的植物相互作用，而萜烯 (terpene)、茉莉酸甲酯 (methyl jasmonate; MeJA)、甲基水楊酸 (Methyl Salicylate; MeSA) 或綠葉揮發物 (green-leaf volatiles) 係屬揮發性較低，能夠作為長距離訊號傳遞 (War *et al*. 2011)。Zhao *et al*. (2020) 研究顯示茶樹在寒害逆境下會釋放橙花叔醇 (nerolidol)、香葉醇 (geraniol)、芳樟醇 (linalool) 及 MeSA，這些 pVOCs 可透過 C-repeat-binding factor dependent pathway 進行訊號傳遞，進而誘導鄰近茶樹的抗寒能力。

吸引授粉者與種子傳播者 (pollination & seed dispersal)

開花植物可透過花朵釋放多樣化且高劑量的 pVOCs 吸引蜜蜂、蝴蝶等授粉傳播者，以確保植物能有效繁殖，其藉由花朵內組織特異性與發育調控所產生的氣味，以提供有關著陸與食物機會的精細空間資訊作為授粉傳播者長、短距離的引誘劑 (Raguso 2008; Dudareva *et al*. 2013)。不同的生殖器官 (如花瓣、萼片、花粉及花蜜等) 所釋放的 pVOCs 也有所差異，此種特性與優先吸引的昆蟲或化學防禦有關 (Farré-Armengol *et al*. 2013)。Byers *et al*. (2014) 報告顯示 *Mimulus lewisii* 花朵所釋放的 pVOCs 為檸檬烯 (limonene)、月桂烯 (myrcene) 及羅勒烯 (ocimene)，其中又以檸檬烯為吸引大黃蜂 (*Bombus vosnesenskii*) 授粉最為關鍵。另一方面，果實成熟後也會釋放 pVOCs 以吸引動物攝食，進而促進種子傳播並有助於生態系內植物族群的空間移動 (Dudareva *et al*. 2013)。Youngsteadt *et al*. (2008) 研究指出附生植物 (*Peperomia macrostachyam*) 種子所釋放的 pVOCs 混合物會吸引亞馬遜雨林的巨山蟻 (*Camponotus femoratus*) 對種子的收集行為，進而促進種子傳播。

促進作物生長與適應環境逆境

pVOCs 可能具有植物生長調節作用，藉由

與其他代謝物與植物荷爾蒙協同作用，共同參與調節植物老化 (senescence) 過程，且 pVOCs 也可產生植物間的相剋作用 (allelopathy) 抑制鄰近雜草種子的發芽與根部生長，進而提升自身在有限資源下的競爭力與適應能力 (Brilli *et al*. 2019)。Dani *et al*. (2016) 研究顯示異戊二烯類 (isoprenoids)、類胡蘿蔔素 (carotenoids) 與細胞分裂素 (cytokinins) 在成熟葉片中共同維持光合系統 (photosystems) 結構與功能的穩定，有效降低活性氧類 (reactive oxygen species; ROS) 所造成的氧化損傷，進而延長葉片功能壽命，提升植物逆境適應力與作物整體生產力。Gfeller *et al*. (2019) 研究指出斑矢車菊 (*Centaurea stoebe*) 根部所釋放的pVOCs含有豐富的倍半萜烯 (sesquiterpene)，以 (E)-β-caryophyllene 與 daucadiene 為主要成分，其會影響鄰近植物的種子發芽與生長，進而改變植物群落的結構分佈。Srikanth *et al*. (2024) 報告顯示植物釋放的異戊二烯 (isoprene) 具有清除逆境所產生之 ROS 的能力，並能抑制一氧化氮 (nitric oxide)、過氧化氫 (hydrogen peroxide)、臭氧 (ozone) 及單線態氧 (singlet oxygen) 的累積，進而減少細胞氧化損傷，提升植物耐高溫與抗氧化逆境的能力。綜合文獻研究顯示，pVOCs 具有穩定細胞膜結構與清除 ROS 的能力，有效減緩因環境逆境所造成的細胞損傷，其主要透過降低膜脂質過氧化程度、維持葉綠體細胞膜功能與抑制 ROS 累積，進而提升植物對逆境的適應能力 (Loreto & Velikova 2001; Velikova *et al*. 2011; Brilli *et al*. 2019)。

提高農產品品質 (food quality improvement)

pVOCs 為農產品的香氣、風味及品質之指標之一，如檸檬烯 (limonene) 為柑橘類水果的主要芳香成分 (Viuda-Martos *et al*. 2009)；而己烯醛 (hexenal) 是櫻桃番茄 (*Lycopersicum esculentum*) 的主要香氣成分 (Selli *et al*. 2014)；咖啡豆烘焙過程中所產生的 pVOCs 則為決定咖啡品質的重要因素，其中又以含硫化合物 (sulfur-containing compounds) 與吡嗪類 (pyrazines) 被認為是影響咖啡風味的成分 (Sunarharum *et al*. 2014)。此外，揮發性成分含有重要風味，也有助於人體健康等益處 (Ayseli & Ayseli 2016)。Park *et al*. (2012) 研究指出芳樟醇與其降解產物 α-松油醇 (α-terpineol) 對牙周病菌 (periodontopathic) 與致齲菌 (cariogenic bacteria) 具有強效的抗菌活性。Miyazawa *et al*. (2016) 研究顯示紅鳳菜精油可抑制乙醯膽鹼酯酶 (acetylcholinesterase; AChE) 的活性，且倍半萜類抑制 AChE 的活性高於單萜類化合物。綜整文獻有關植物揮發性有機化合物的生物性功能，詳見表 1。

植物揮發性成分的生合成

由於 pVOCs 具備低分子量、親脂性以及在常溫常壓下具高蒸氣壓等特性，使其得以穿透細胞膜並釋放至外界環境 (Pichersky *et al*. 2006)。pVOCs 的生合成主要依賴碳、氮與硫元素，以及初級代謝所提供的能量來源，而其生合成來源可分為幾類，包含萜類化合物 (terpenoids)、苯丙烷類/苯類 (phenylpropanoids/benzenoids) 化合物、脂肪酸 (fatty acid) 及胺基酸 (amino acid) 衍生物 (Dudareva *et al*. 2006, 2013)，有關植物揮發性成分之簡易生合成途徑，如圖 1。萜類化合物 (terpenoids) 是植物次級代謝物中數量最多的一類，如植物精油乃存在於植物體內的天然有機物質，是由多種揮發性成分所構成的混合物，其主要成分即為各類萜類化合物，如異戊二烯類 (isoprenoids, C_5)、單萜類 (monoterpenoids, C_{10}) 及倍半萜類 (sesquiterpenoids, C_{15}) 等，這些萜類化合物主要由碳水化合物透過糖解作用生成丙酮酸 (pyruvate)，再經由細胞質的甲羥戊酸 (mevalonic acid; MVA) 與質體的甲基赤蘚糖醇磷酸鹽 (methylerythritol phosphate; MEP) 途徑促成之生合成，其中 MVA 途徑會產生揮發性的倍半萜類 (C_{15})，而 MEP 途徑則會產生半萜類 (hemiterpenes, C_5)、單萜類 (C_{10}) 及二萜類 (diterpenes, C_{20}) 的前驅物 (Holopainen & Gershenzon 2010; Dudareva *et al*. 2013)。

第二大類 pVOCs 為苯丙烷類與苯類化合物 (phenylpropanoids/benzenoids)，其生合成主要源自芳香族胺基酸的苯丙胺酸 (phenylalanine; Phe)，並經由質體中的莽草酸/苯丙胺

表 1. 綜整文獻有關植物揮發性有機化合物的生物性功能。

Table 1. Comprehensive references regarding the biological functions of plant volatile organic compounds (pVOCs).

Plant	pVOC compounds	Biological functions	References
Cherry tomato; stone fruits	*trans*-2-hexenal (*Z*)-3-hexenal (*E*)-2-hexenal	(*Z*)-3-hexenal and (*E*)-2-hexenal were the primary aroma-active compounds in cherry tomatoes. *Trans*-2-hexenal exhibits the strongest antifungal activity against *Monilinia laxa*.	Neri *et al*. 2007; Selli *et al*. 2014
Citrus fruits; tea	linalool	It exhibits potent antifungal activity, effectively preventing citrus postbloom fruit drop caused by *Colletotrichum acutatum*, and functions as an inducible volatile that triggers interplant communication.	Marques *et al*. 2014; Zhao *et al*. 2020
Citrus fruits; *Mimulus lewisii*	limonene	It is the primary aromatic component of citrus fruits and plays a role in controlling mealybugs and scale insects, while also acting as a driver of pollinator-based speciation.	Hollingsworth 2005; Viuda-Martos *et al*. 2009; Byers *et al*. 2014
Pines; tomato	2-carene 3-carene	2-Carene has repellent and toxic effects on insect species and constitutes the major component of the tomato floral scent. 3-Carene exhibits strong antifungal activity and weak nematicidal activity in pine.	Morse *et al*. 2012; Hwang *et al*. 2021
Pines; tomato	α-pinene	It exhibits repellent and toxic effects on insect species and inhibits the feeding activity of bark beetles.	Morse *et al*. 2012; Xu *et al*. 2014
Rice; spotted knapweed	(*E*)-β-caryophyllene	It plays a role in indirect defense by attracting parasitoid wasps and may further support the germination and growth of neighboring plants.	Cheng *et al*. 2007; Gfeller *et al*. 2019
Stone fruits	citral	It moderately inhibits both conidial germination and mycelial growth of *Monilinia laxa*.	Neri *et al*. 2007
Stone fruits	carvacrol	It exhibits inhibitory effects on the mycelial growth of *Monilinia laxa*.	Neri *et al*. 2007
Tea	nerolidol	Acts as an inducible volatile signaling neighboring plants to respond to cold stress.	Zhao *et al*. 2020
Tea	geraniol	Acts as an inducible volatile signaling neighboring plants to respond to cold stress.	Zhao *et al*. 2020
Tomato	p-cymene	It exhibits repellent and toxic effects on insect species.	Morse *et al*. 2012
Tomato	β-phellandrene	It has repellent and toxic effects on insect species and constitutes the major component of the tomato floral scent.	Morse *et al*. 2012

酸 (shikimate/phenylalanine) 途徑所產生，此途徑起始於赤鮮糖-4-磷酸 (erythrose 4-phosphate) 與磷酸烯醇丙酮酸 (phosphoenolpyruvate; PEP) 之縮合，形成莽草酸 (shikimate) 中間產物，進一步經由 3-dehydroshikimic acid 與 chorismate 等一系列酵素促進反應，最終生成苯丙胺酸 (Phe)。Phe 經由苯丙胺酸脫氨裂解酶 (phenylalanine ammonia lyase; PAL) 作用，轉化為反式肉桂酸 (trans-cinnamic acid)，進一步合成羥基肉桂酸類 (hydroxycinnamic acids)，並經由甲基化 (methylation) 與羥基化 (hydroxylation) 修飾後，產生多種具揮發性的羥基肉桂酸衍生物、醛類及醇類等芳香化合物 (Dudareva *et al*. 2013; Niinemets *et al*. 2013)。

第三大類 pVOCs 為脂肪酸衍生物 (fatty acid derivatives)，如 1-己醛 (1-hexanal)、順式-3-己烯醇 (*cis*-3-hexenol)、壬醛 (nonanal) 及 MeJA 等。此類揮發物主要由乙醯輔酶 A (acetyl-CoA) 為起始物，進行脂肪酸生合成，產生 C_{18} 不飽和脂肪酸，如亞麻油酸 (linoleic acid) 與次亞麻油酸 (linolenic acid)，這些不飽和脂肪酸為脂肪酸衍生 pVOCs 的前驅物，經由氧化進入脂氧合酶

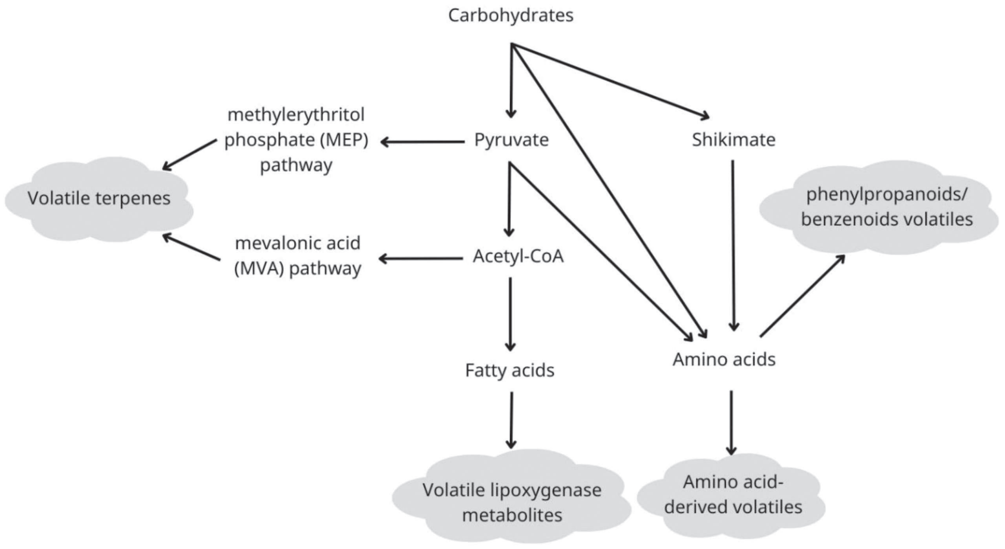

圖 1. 植物揮發性成分之簡易生合成途徑。
Fig. 1. Simplified biosynthetic pathways of plant volatile organic compounds (pVOCs).

(lipoxygenase; LOX) 途徑產生 9-hydroperoxy 與 13-hydroperoxy 中間產物，再進一步由過氧化物水解酶 (hydroperoxide lyases; HPLs) 與醇脫氫酶 (alcohol dehydrogenases; ADHs) 等酵素的作用下，轉化為多種具有揮發性的醛類與醇類化合物，此類 pVOCs 通常被稱為綠葉揮發物 (green leaf volatiles; GLVs)，其生合成多發生於植物綠色器官受損時，不僅參與植物防禦反應，也是許多蔬果呈現新鮮綠色氣味的主要來源 (Feussner & Wasternack 2002; Bruinsma *et al*. 2009)。

第四大類 pVOCs 為胺基酸衍生物 (amino acid derivatives)，包含醛、醇、酯、酸以及含氮與含硫的揮發物均來自胺基酸，如丙胺酸 (alanine)、擷胺酸 (valine)、白胺酸 (leucine)、異白胺酸 (isoleucine) 及甲硫胺酸 (methionine) 等胺基酸或其生物合成中間產物，當胺基酸經脫氨基 (deamination) 或轉氨基 (transamination) 後生成 α-酮酸 (α-keto acid)，再經由脫羧 (decarboxylation)、還原 (reductions)、氧化 (oxidations) 及酯化 (esterification) 等作用產生醛、酸、醇、酯，此類 pVOCs 主要為花香與果香中的揮發性化合物 (Dudareva *et al*. 2006; Knudsen *et al*. 2006)。

溫度對植物揮發性成分的影響

植物揮發性氣體的組成與植物種類 (species)、器官 (organs)、發育階段 (developmental stages) 及環境條件 (environmental conditions) 有關，在果實特定的發育階段與植物不同的組織部位 (如葉、根及花) 等，均可檢測到揮發性化合物的產生與釋放 (Possell & Loreto 2013; Ren *et al*. 2014; Chiu *et al*. 2017)。另一方面，環境因子對揮發性成分的影響，包含光照強度、二氧化碳濃度、溫度、相對濕度及營養等 (Staudt & Bertin 1998; Gouinguené & Turlings 2002; Ren *et al*. 2014)，而溫度對 pVOCs 的合成與釋放乃是關鍵環境因子之一 (Guenther *et al*. 2012; Grote *et al*. 2013; Copolovici & Niinemets 2016)。Harley (2013) 研究顯示，溫度會決定植體中 pVOCs 的氣相-液相分布情形，即當溫度升高時，揮發性化合物會轉化成氣體並從植體中釋放出去。此外，葉面特徵、空氣溫度、葉面溫度以及揮發物的物理化學性質是決定葉面 pVOCs 沉積與再釋放的重要因素 (Schaub *et al*. 2010; Niinemets *et al*. 2014)。Gouinguené & Turlings (2002) 研究顯示玉米 (*Zea mays*) 植株的氣味主要由萜烯

(terpenoids) 與吲哚 (indoles) 所組成，不同環境因子會影響揮發性氣體的釋放量，而在 22 與 27℃會有最高的釋放量，且溫度亦會改變氣味成分的含量，研究發現在 37℃高溫下 β-caryophyllene 比例最高，而 geranyl acetate 含量則在 22℃下較多。Chang *et al*. (2005) 研究指出羅勒 (*Ocimum basilicum* L.) 最適生長溫度為 25℃，在此溫度環境下會有最佳的生長參數與揮發性化合物含量；此外，溫度亦會影響揮發性成分的組成，如在 25℃下會使 eugenol 與 *cis*-ocimene 含量增加，而 15℃下則會累積 camphor 與 *trans*-β-farnesene 的含量。Prodhan *et al*. (2017) 報告指出除了基因型會影響香米氣味之外，揮發性化合物的組成亦決定香米的香氣狀態，且環境溫度也會影響揮發性成分的組成與含量變化進而改變香氣表現，其發現在 25℃下可獲得最佳的香氣官能品評。Ho *et al*. (2021) 研究顯示不同的栽培溫度會影響紅鳳菜 (*Gynura bicolor* DC) 葉片的單萜類 (monoterpenoids) 與倍半萜類 (sesquiterpenoids) 組成含量，其中總單萜類含量在 20 與 25℃最高，而總倍半萜類含量則在 30 與 35℃最佳，且 α-pinene 與 α-humulene 的相對含量在 20℃最高，而 copaene 則在 35℃最好。綜合文獻研究可知，溫度是影響 pVOCs 釋放量、成分含量及化學組成的關鍵因素。

結語

綜合上述研究顯示，pVOCs 在農業中具有多種潛在應用性，如天敵誘導與害蟲防治、增強作物抗病能力、促進作物生長及提高品質等，且 pVOCs 還可作為天然殺蟲劑或驅避劑等友善環境的農藥替代品，以減少田間化學農藥使用。然而，pVOCs 具有易揮發與高生物降解性，且易受環境因素影響，導致 pVOCs 的持續性與穩定性不足，再加上 pVOCs 的作用範圍有限，難以在田間栽培中發揮穩定效果。另一方面，pVOCs 在應用時可能會影響非目標生物 (如授粉昆蟲)，因此需進一步評估生態安全性，且萃取或合成 pVOCs 成本較高，目前商業應用仍受到限制。目前 pVOCs 可作為生物防治與有機農業應用的輔助策略，但尚未能完全替代傳統農藥，若要擴大 pVOCs 的應用，仍需克服上述限制條件且進一步研究與技術優化。

引用文獻

Ali, J. G., H. T. Alborn, R. Campos-Herrera, F. Kaplan, L. W. Duncan, C. Rodriguez-Saona, ... L. L. Stelinski. 2012. Subterranean, herbivore-induced plant volatile increases biological control activity of multiple beneficial nematode species in distinct habitats. PLoS One 7:e38146. doi:10.1371/journal.pone.0038146

Ayseli, M. T. and Y. İ. Ayseli. 2016. Flavors of the future: Health benefits of flavor precursors and volatile compounds in plant foods. Trends Food Sci. Technol. 48:69–77. doi:10.1016/j.tifs.2015.11.005

Baier, P., E. Führer, T. Kirisits, and S. Rosner. 2002. Defence reactions of Norway spruce against bark beetles and the associated fungus *Ceratocystis polonica* in secondary pure and mixed species stands. For. Ecol. Manage. 159:73–86. doi:10.1016/S0378-1127(01)00711-3

Brilli, F., F. Loreto, and I. Baccelli. 2019. Exploiting plant volatile organic compounds (VOCs) in agriculture to improve sustainable defense strategies and productivity of crops. Front. Plant Sci. 10:264. doi:10.3389/fpls.2019.00264

Bruinsma, M., M. A. Posthumus, R. Mumm, M. J. Mueller, J. J. van Loon, and M. Dicke. 2009. Jasmonic acid-induced volatiles of *Brassica oleracea* attract parasitoids: Effects of time and dose, and comparison with induction by herbivores. J. Exp. Bot. 60:2575–2587. doi:10.1093/jxb/erp101

Byers, K. J. R. P., H. D. Bradshaw, and J. A. Riffell. 2014. Three floral volatiles contribute to differential pollinator attraction in monkeyflowers (*Mimulus*). J. Exp. Biol. 217:614–623. doi:10.1242/jeb.092213

Chang, X., P. Alderson, and C. Wright. 2005. Effect of temperature integration on the growth and volatile oil content of basil (*Ocimum basilicum* L.). J. Hortic. Sci. Biotechnol. 80:593–598. doi:10.1080/14620316.2005.11511983

Cheng, A. X., C. Y. Xiang, J. X. Li, C. Q. Yang, W. L. Hu, L. J. Wang, ... X. Y. Chen. 2007. The rice (E)-beta-caryophyllene synthase (OsTPS3) accounts for the major inducible volatile sesquiterpenes. Phytochemistry 68:1632–1641. doi:10.1016/j.phytochem.2007.04.008

Chiu, Y. T., H. C. Chen, and C. Chang. 2017. The variation of *Oncidium* Rosy Sunset flower volatiles with daily rhythm, flowering period, and flower parts. Molecules 22:1468. doi:10.3390/mole-

cules22091468

Copolovici, L. and Ü. Niinemets. 2016. Environmental impacts on plant volatile emission. p.35–59. *in*: Deciphering Chemical Language of Plant Communication. (Blande, J. D. and R. Glinwood, eds.) Springer International Publishing, Cham. 326 pp.

Dani, K. G. S., S. Fineschi, M. Michelozzi, and F. Loreto. 2016. Do cytokinins, volatile isoprenoids and carotenoids synergically delay leaf senescence? Plant Cell Environ. 39:1103–1111. doi:10.1111/pce.12705

Dudareva, N., F. Negre, D. A. Nagegowda, and I. Orlova. 2006. Plant volatiles: Recent advances and future perspectives. Crit. Rev. Plant Sci. 25:417–440. doi:10.1080/07352680600899973

Dudareva, N., A. Klempien, J. K. Muhlemann, and I. Kaplan. 2013. Biosynthesis, function and metabolic engineering of plant volatile organic compounds. New Phytol. 198:16–32. doi:10.1111/nph.12145

Farré-Armengol, G., I. Filella, J. Llusia, and J. Peñuelas. 2013. Floral volatile organic compounds: Between attraction and deterrence of visitors under global change. Perspect. Plant Ecol. Evol. Syst. 15:56–67. doi:10.1016/j.ppees.2012.12.002

Feussner, I. and C. Wasternack. 2002. The lipoxygenase pathway. Annu. Rev. Plant Biol. 53:275–297. doi:10.1146/annurev.arplant.53.100301.135248

Gfeller, V., M. Huber, C. Förster, W. Huang, T. G. Köllner, and M. Erb. 2019. Root volatiles in plant–plant interactions I: High root sesquiterpene release is associated with increased germination and growth of plant neighbours. Plant Cell Environ. 42:1950–1963. doi:10.1111/pce.13532

Giorgi, A., A. Manzo, N. Nanayakkarawasam Masachchige Chandrika Nanayakkara, L. Giupponi, M. Cocucci, and S. Panseri. 2015. Effect of biotic and abiotic stresses on volatile emission of *Achillea collina* Becker ex Rchb. Nat. Prod. Res. 29:1695–1702. doi:10.1080/14786419.2014.997725

Gols, R. 2014. Direct and indirect chemical defences against insects in a multitrophic framework. Plant Cell Environ. 37:1741–1752. doi:10.1111/pce.12318

Gouinguené, S. P. and T. C. J. Turlings. 2002. The effects of abiotic factors on induced volatile emissions in corn plants. Plant Physiol. 129:1296–1307. doi:10.1104/pp.001941

Grote, R., R. K. Monson, and Ü. Niinemets. 2013. Leaf-level models of constitutive and stress-driven volatile organic compound emissions. p.315–355. *in*: Biology, Controls and Models of Tree Volatile Organic Compound Emissions. (Niinemets, Ü. and R. K. Monson, eds.) Springer Netherlands. Dordrecht, The Netherlands. 547 pp.

Guenther, A. B., X. Jiang, C. L. Heald, T. Sakulyanontvittaya, T. Duhl, L. K. Emmons, and X. Wang. 2012. The model of emissions of gases and aerosols from nature version 2.1 (MEGAN2.1): An extended and updated framework for modeling biogenic emissions. Geosci. Model Dev. 5:1471–1492. doi:10.5194/gmd-5-1471-2012

Harley, P. C. 2013. The roles of stomatal conductance and compound volatility in controlling the emission of volatile organic compounds from leaves. p.181–208. *in*: Biology, Controls and Models of Tree Volatile Organic Compound Emissions. (Niinemets, Ü. and R. K. Monson, eds.) Springer Netherlands. Dordrecht, The Netherlands. 547 pp.

Heil, M. and J. C. Silva Bueno. 2007. Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. Proc. Natl. Acad. Sci. U.S.A. 104:5467–5472. doi:10.1073/pnas.0610266104

Hiltpold, I. and T. C. J. Turlings. 2012. Manipulation of chemically mediated interactions in agricultural soils to enhance the control of crop pests and to improve crop yield. J. Chem. Ecol. 38:641–650. doi:10.1007/s10886-012-0131-9

Ho, C. H., M. H. Yang, and H. L. Lin. 2021. Temperature and different organs create volatile profile differences of edible Gynura [*Gynura bicolor* (Roxb. ex Willd.) DC]. HortScience 56:954–960. doi:10.21273/HORTSCI15851-21

Hollingsworth, R. G. 2005. Limonene, a citrus extract, for control of mealybugs and scale insects. J. Econ. Entomol. 98:772–779. doi:10.1603/0022-0493-98.3.772

Holopainen, J. K. and J. Gershenzon. 2010. Multiple stress factors and the emission of plant VOCs. Trends Plant Sci. 15:176–184. doi:10.1016/j.tplants.2010.01.006

Hwang, H. S., J. Y. Han, and Y. E. Choi. 2021. Enhanced emission of monoterpene 3-carene in *Pinus densiflora* infected by pine wood nematode and characterization of 3-carene Synthase. Forests 12:514. doi:10.3390/f12050514

James, D. G. and T. R. Grasswitz. 2005. Synthetic herbivore-induced plant volatiles increase field captures of parasitic wasps. BioControl. 50:871–880. doi:10.1007/s10526-005-3313-3

Knudsen, J. T., R. Eriksson, J. Gershenzon, and B. Ståhl. 2006. Diversity and distribution of floral scent. Bot. Rev. 72:1–120.

Loreto, F. and V. Velikova. 2001. Isoprene produced by leaves protects the photosynthetic apparatus against ozone damage, quenches ozone products, and reduces lipid peroxidation of cellular membranes. Plant Physiol. 127:1781–1787. doi:10.1104/pp.010497

Marques, J. P. R., L. Amorim, G. J. Silva-Junior, M. B. Spósito, and B. Appezzato-da Gloria. 2014. Structural and biochemical characteristics of citrus flowers associated with defence against a fungal pathogen. AoB Plants 7:plu090. doi:10.1093/aobpla/plu090

McConkey, M. E., J. Gershenzon, and R. B. Croteau. 2000. Developmental regulation of monoterpene biosynthesis in the glandular trichomes of peppermint. Plant Physiol. 122:215–224. doi:10.1104/pp.122.1.215

Mita, E., C. Tsitsimpikou, L. Tsiveleka, P. V. Petrakis, A. Ortiz, C. Vagias, and V. Roussis. 2002. Seasonal variation of oleoresin terpenoids from *Pinus halepensis* and *Pinus pinea* and host selection of the scale insect *Marchalina hellenica* (*Homoptera*, *Coccoidea*, *Margarodidae*, *Coelostonidiinae*). Holzforschung 56:572–578. doi:10.1515/HF.2002.087

Miyazawa, M., H. Nakahashi, A. Usami, and N. Matsuda. 2016. Chemical composition, aroma evaluation, and inhibitory activity towards acetylcholinesterase of essential oils from *Gynura bicolor* DC. J. Nat. Med. 70:282–289. doi:10.1007/s11418-015-0961-1

Morse, A., P. Kevan, L. Shipp, S. Khosla, and B. McGarvey. 2012. The impact of greenhouse tomato (Solanales: Solanaceae) floral volatiles on bumble bee (Hymenoptera: Apidae) pollination. Environ. Entomol. 41:855–864. doi:10.1603/EN11234

Neri, F., M. Mari, S. Brigati, and P. Bertolini. 2007. Fungicidal activity of plant volatile compounds for controlling *Monilinia laxa* in stone fruit. Plant Dis. 91:30–35. doi:10.1094/PD-91-0030

Niinemets, Ü., A. Kännaste, and L. Copolovici. 2013. Quantitative patterns between plant volatile emissions induced by biotic stresses and the degree of damage. Front. Plant Sci. 4:262. doi:10.3389/fpls.2013.00262

Niinemets, Ü., S. Fares, P. Harley, and K. J. Jardine. 2014. Bidirectional exchange of biogenic volatiles with vegetation: Emission sources, reactions, breakdown and deposition. Plant Cell Environ. 37:1790–1809. doi:10.1111/pce.12322

Ninkovic, V., D. Markovic, and M. Rensing. 2021. Plant volatiles as cues and signals in plant communication. Plant Cell Environ. 44:1030–1043. doi:10.1111/pce.13910

Park, S. N., Y. K. Lim, M. O. Freire, E. Cho, D. Jin, and J. K. Kook. 2012. Antimicrobial effect of linalool and α-terpineol against periodontopathic and cariogenic bacteria. Anaerobe 18:369–372. doi:10.1016/j.anaerobe.2012.04.001

Pichersky, E., J. P. Noel, and N. Dudareva. 2006. Biosynthesis of plant volatiles: Nature's diversity and ingenuity. Science 311:808–811. doi:10.1126/science.1118510

Possell, M. and F. Loreto. 2013. The role of volatile organic compounds in plant resistance to abiotic stresses: Responses and mechanisms. p.209–235. *in*: Biology, Controls and Models of Tree Volatile Organic Compound Emissions. (Niinemets, Ü. and R. K. Monson, eds.) Springer Netherlands, Dordrecht. 547 pp.

Prodhan, Z. H., G. Faruq, K. A. Rashid, and R. M. Taha. 2017. Effects of temperature on volatile profile and aroma quality in rice. Int. J. Agric. Biol. 19:1065–1072. doi:10.17957/IJAB/15.0385

Raguso, R. A. 2008. Wake up and smell the roses: The ecology and evolution of floral scent. Annu. Rev. Ecol. Evol. Syst. 39:549–569. doi:10.1146/annurev.ecolsys.38.091206.095601

Ren, J., S. Guo, Q. Cheng, Y. Shen, and H. Q. Feng. 2014. Synergistic effects of CO_2 and LED lighting on accumulation of terpenes in roots of *Gynura bicolor*. Chin. Herb. Med. 6:228–236. doi:10.1016/S1674-6384(14)60033-2

Schaub, A., J. D. Blande, M. Graus, E. Oksanen, J. K. Holopainen, and A. Hansel. 2010. Real-time monitoring of herbivore induced volatile emissions in the field. Physiol. Plant. 138:123–133. doi:10.1111/j.1399-3054.2009.01322.x

Selli, S., H. Kelebek, M. T. Ayseli, and H. Tokbas. 2014. Characterization of the most aroma-active compounds in cherry tomato by application of the aroma extract dilution analysis. Food Chem. 165:540–546. doi:10.1016/j.foodchem.2014.05.147

Srikanth, P., A. Maxton, S. A. Masih, A. Sofo, and N. A. Khan. 2024. Isoprene: An antioxidant to guard plants against stress. Int. J. Plant Biol. 15:161–174. doi:10.3390/ijpb15010013

Staudt, M. and N. Bertin. 1998. Light and temperature dependence of the emission of cyclic and acyclic monoterpenes from holm oak (*Quercus ilex* L.) leaves. Plant Cell Environ. 21:385–395. doi:10.1046/j.1365-3040.1998.00288.x

Sunarharum, W. B., D. J. Williams, and H. E. Smyth. 2014. Complexity of coffee flavor: A compositional and sensory perspective. Food Res. Int. 62:315–325. doi:10.1016/j.foodres.2014.02.030

Unsicker, S. B., G. Kunert, and J. Gershenzon. 2009. Protective perfumes: The role of vegetative volatiles in plant defense against herbivores. Curr. Opin. Plant Biol. 12:479–485. doi:10.1016/j.pbi.2009.04.001

Vassão, D. G., D. R. Gang, T. Koeduka, B. Jackson, E. Pichersky, L. B. Davin, and N. G. Lewis. 2006.

Chavicol formation in sweet basil (*Ocimum basilicum*): Cleavage of an esterified C9 hydroxyl group with NAD(P)H-dependent reduction. Org. Biomol. Chem. 4:2733–2744. doi:10.1039/B605407B

Velikova, V., Z. Várkonyi, M. Szabó, L. Maslenkova, I. Nogues, L. Kovács, ... F. Loreto. 2011. Increased thermostability of thylakoid membranes in isoprene-emitting leaves probed with three biophysical techniques. Plant Physiol. 157:905–916. doi:10.1104/pp.111.182519

Viuda-Martos, M., Y. Ruiz-Navajas, J. Fernández-López, and J. A. Pérez-Álvarez. 2009. Chemical composition of mandarin (*C. reticulata* L.), grapefruit (*C. paradisi* L.), lemon (*C. limon* L.) and orange (*C. sinensis* L.) essential oils. J. Essent. Oil-Bear. Plants 12:236–243. doi:10.1080/0972060X.2009.10643716

War, A. R., H. C. Sharma, M. G. Paulraj, M. Y. War, and S. Ignacimuthu. 2011. Herbivore induced plant volatiles: Their role in plant defense for pest management. Plant Signal. Behav. 6:1973–1978. doi:10.4161/psb.6.12.18053

Xu, B. B., Z. D. Liu, and J. H. Sun. 2014. The effects of α-pinene on the feeding performance and pheromone production of *Dendroctonus valens*. Entomol. Exp. Appl. 150:269–278. doi:10.1111/eea.12161

Youngsteadt, E., S. Nojima, C. Häberlein, S. Schulz, and C. Schal. 2008. Seed odor mediates an obligate ant-plant mutualism in Amazonian rainforests. Proc. Natl. Acad. Sci. U.S.A. 105:4571–4575. doi:10.1073/pnas.0708643105

Zhao, M., L. Wang, J. Wang, J. Jin, N. Zhang, L. Lei, ... C. Song. 2020. Induction of priming by cold stress via inducible volatile cues in neighboring tea plants. J. Integr. Plant Biol. 62:1461–1468. doi:10.1111/jipb.12937

Exploring the Biological Functions of Plant Volatile Organic Compounds

Chia-Hsun Ho[1,*], Man-Hsia Yang[2], Chiao-Ling Hsiao[2], and Ya-Ling Hou[1]

Abstract

Ho, C. H., M. H. Yang, C. L. Hsiao, and Y. L. Hou. 2025. Exploring the biological functions of plant volatile organic compounds. J. Taiwan Agric. Res. 74(2):141–150.

Plant volatile organic compounds (pVOCs) exhibit various biological functions in ecosystems. These include activating plant defense mechanisms, facilitating plant-to-plant signaling, aiding in pollination and seed dispersal, promoting crop growth and environmental adaptation, and enhancing agricultural product quality. When herbivorous insects attack plants, they induce plants to release specific volatile compounds, known as herbivore-induced plant volatiles (HIPVs), which attract natural enemies of pests and trigger defense responses in neighboring plants. Additionally, pVOCs involve plant-to-plant communication, enhancing the resistance of surrounding plants under stresses. The biosynthesis of pVOCs originates from multiple biochemical pathways and can be categorized into four major groups: terpenoids, phenylpropanoids/benzenoids, fatty acid derivatives, and amino acid derivatives. On the other hand, environmental factors influence the emission levels, composition, and chemical properties of pVOCs, with temperature being a key determinant. The pVOCs show significant potential as biocontrol agents for organic agriculture. However, their high volatility, rapid biodegradability, sensitivity to environmental conditions, and high production costs pose challenges to their widespread agricultural application. Further research and technical improvements are needed to overcome limitations before pVOCs can effectively replace traditional pesticides in sustainable agriculture.

Key words: Volatile organic compounds, Biological functions, Terpenoids, Biosynthesis, Temperature.

Received: February 21, 2025; Accepted: April 7, 2025.
* Corresponding author, e-mail: chia0423@tari.gov.tw
1 Assistant Research Fellows, Crop Science Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
2 Associate Research Fellows, Crop Science Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):151–159 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0005

Research Article

Evaluation of Reflectometry and Refractometry for Rapid Sugar Detection in Sweet Potatoes

Hui-Ying Hou[1], Che-Lun Huang[2], I-Chi Yeh[3], and Yung-Chang Lai[4,*]

Abstract

Hou, H. Y., C. L. Huang, I. C. Yeh, and Y. C. Lai. 2025. Evaluation of reflectometry and refractometry for rapid sugar detection in sweet potatoes. J. Taiwan Agric. Res. 74(2):151–159.

Sugar content, a key quality attribute of sweet potatoes, is influenced by cultivar, maturity, storage conditions, and processing methods. This study aimed to develop efficient methods for measuring sweet potato sugar content using the reflectometer and refractometer. Ten sweet potato cultivars with diverse tuber flesh colors were evaluated in raw and baked forms. A simplified water extraction method facilitated analysis with both instruments. The RQFlex20 reflectometer, coupled with Reflectoquant sucrose and total sugar (glucose and fructose) test kits, was used to measure the sugar concentrations in sweet potatoes. Results demonstrated two linear regression models between the reflectometer and the reference method for the corresponding sugar contents, with coefficients of determination (R^2) of 0.95 and 0.86, respectively. Additionally, the refractometer measured total sugar content, exhibiting a strong linear regression (R^2 = 0.91) with the reference method. Furthermore, it could predict maltose content in baked sweet potatoes with a linear regression model (R^2 = 0.90), thereby overcoming a limitation of the RQFlex20 without maltose. This study demonstrated that reflectometry and refractometry offered a rapid and cost-effective method for measuring sugar content in sweet potatoes. This provided a valuable alternative to traditional high-performance liquid chromatography (HPLC) techniques, particularly for the agricultural and food processing industries.

Key words: Sweet potato, Sugar content, Reflectometer, Refractometer.

INTRODUCTION

Sweet potato (*Ipomoea batatas* (L.) Lam.), a member of the Convolvulaceae family, is an important global crop with a worldwide production of approximately 90 million megagrams and grows particularly vigorously in tropical and subtropical regions (Šlosár *et al*. 2019; Allan *et al*. 2024; Food and Agriculture Organization of the United Nations, https://www.fao.org/faostat/en/#data/QCL). This root vegetable, known for its large, starchy, sweet-tasting storage roots, is rich in vitamins, minerals, dietary fiber, and bioactive compounds with various health benefits (Lai *et al*. 2016; Yoon *et al*. 2018). Sweet potatoes are valued for their sweetness, derived from endogenous sugars such as sucrose, glucose, and fructose. Maltose, hydrolyzed from starch by amylase enzymes during cooking, also contributes to their overall sweetness (Laurie

Received: October 18, 2024; Accepted: December 20, 2024.
* Corresponding author, e-mail: davidlai489@gmail.com
[1] Assistant Research Fellow, Department of Agronomy, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.
[2] Associate Research Fellow, Department of Agronomy, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.
[3] Former Assistant Research Fellow, Department of Agronomy, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.
[4] Research Fellow and Division Director, Department of Agronomy, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.

et al. 2013; Kitahara *et al*. 2017; Nakamura *et al*. 2018; Allan *et al*. 2024). Several factors affect the sweetness, including cultivars, farming systems, postharvest processes, and food processing. The variation in sweetness and flavor among different sweet potato cultivars is notable. Cultivation conditions, such as fertilizer application and harvest timing, impact their sugar content and quality (Adu-Kwarteng *et al*. 2014; Krochmal-Marczak *et al*. 2020). Storage conditions are also crucial factors influencing the sugar content of sweet potatoes (Rees *et al*. 2003; Huang *et al*. 2014). Additionally, cooking methods, particularly baking, significantly alter sweet potatoes' sugar composition and sensory attributes (Adu-Kwarteng *et al*. 2014; Wei *et al*. 2017). Therefore, the sugar content in sweet potatoes has been considered as an index for quality.

Several methods are used to determine sugar content including indirect physical, enzymatic, or semi-empirical chemical approaches. These methods can be affected by various factors like color development wavelength, time, temperature, and detection range, leading to inaccuracies (Buiarelli *et al*. 2016; Yue *et al*. 2022). For the phenol-sulfuric acid method, calculating the specific total sugar content requires a standard curve based on standard monosaccharides, which can result in significant errors in sugar content determination (Yue *et al*. 2022). Other methods directly quantify specific sugars or total sugar content. High-performance liquid chromatography (HPLC) is a powerful analytical technique for determining sugar content due to its specificity, ability to simultaneously analyze multiple sugars, accuracy, and precision (Wei *et al*. 2017). It is the preferred method for most studies analyzing sugars in sweet potatoes (Chan *et al*. 2014; Huang *et al*. 2014; Krochmal-Marczak *et al*. 2020; Allan *et al*. 2024), but it requires a substantial upfront investment in equipment and often necessitates specialized training for operators.

Some studies have also employed alternative methods, such as using a refractometer (Suárez *et al*. 2016; Šlosár *et al*. 2019; Takahama *et al*. 2021). The refractometer is a widely used optical instrument for measuring the total soluble solids (Jaywant *et al*. 2022). The Merck Millipore RQFlex/Reflectoquant system is a portable instrument to analyze sucrose and total reducing sugars in plant juice. It utilizes glucose oxidase-peroxidase test strips for colorimetric detection, with the reflectometer measuring reflected light to determine sugar concentrations (Helgerud *et al*. 2016). Although commercially available, its application for quantifying sugar content in sweet potatoes remains relatively underexplored.

This study aims to develop a simple, cost-effective, and field-friendly method for rapidly detecting the sugar content of sweet potatoes. This method, utilizing a reflectometer and a refractometer, offers a promising alternative to existing approaches, facilitating faster decision-making for farmers and processors at the point of demand.

MATERIALS AND METHODS

Materials

Roots from 10 sweet potato varieties (Table 1), including the two major cultivars 'Tainung 57' and 'Tainung 66', were selected and grown separately during the fall (2022 and 2023) and summer 2023 cropping seasons at the Chiayi Agricultural Experiment

Table 1. Flesh color of sweet potato cultivars used in this research.

Cultivars	Tuber flesh color
Tainung 10	White
Tainung 31	White
Tainung 57	Yellow
Tainung 66	Red
Tainung 73	Purple
Tainung 74	Yellow
Kokei 14	Beige
Benimasari	Yellow
Beniharuka	Yellow
Suzuhokkuri	Yellow

Branch in Chiayi, Taiwan, following standard commercial cultivation practices. To obtain data on different sugar content, samples were collected periodically during the pre-harvest and post-harvest periods. The pre-harvest period spanned 2.5 mo before harvest, while the post-harvest period extended up to 4 mo after harvest. Samples were then divided into raw and baked treatments for analysis.

Baking treatment

Roots were baked on a stainless-steel tray in an electric oven (NB-H3801, Panasonic Taiwan Co., Ltd., New Taipei, Taiwan) at 200℃ for 60 min, following the method described by Huang *et al*. (2014). After baking, the sweet potatoes were placed on a stainless-steel plate to cool.

Sample preparation

Raw samples of even size and shape were selected, washed with tap water, peeled, and then mashed by a grater. Baked samples were peeled and mashed using a mortar and pestle. To ensure consistency, only the middle section of each root was used. Moisture content was calculated as the percentage ratio of dry weight to fresh weight following the method outlined by Lai *et al*. (2013). It was subsequently used to calculate sugar content on a dry weight basis.

Method for sugar extraction

The extraction method depended on the analysis technique, utilizing either water or ethanol extraction (Fig. 1). Each sample was extracted in triplicate to ensure accuracy.

For water extraction, 3 g of sweet potato mash was mixed with 9 mL of ultrapure water in a centrifuge tube, shaken vigorously for 20 s, allowed to stand for 5 min, and then filtered by Whatman No. 4 filter paper. The collected filtrate was then used for analysis with a reflectometer and a refractometer.

For ethanol extraction, adapted from Chan *et al*. (2014), 2 g of sweet potato mash was mixed with 10 mL of 80% ethanol in a glass tube. The mixture was then heated at 80℃ for 45 min, and 5 mL of 80% ethanol was added every 15 min. After heating, the mixture was filtered using Whatman No. 4 filter paper, diluted to 20 mL with 80% ethanol, and further filtered through a 0.22 μm membrane filter. The final filtrate was used for HPLC analysis.

Reference measurement

The HPLC system contained a pump (Model CM-5110, Hitachi, Ltd., Tokyo, Japan), a manual sample injector (Rheodyne 7725i, Thermo Scientific, Waltham, MA, USA), a polymer-based hydrophilic interaction liquid chromatography (HILIC) column (Asahipak NH2P-50 4E, 4.6 mm i.d. × 250 mm, 5 μm, Shodex, New York, NY, USA), and an evaporative light scattering detector (Sedex LT-ELSD Model 85LT, Sedere, Olivet, France). The mobile phase was a mixture of ultrapure water (20%) and acetone (80%), and the column temperature was maintained at 45℃. The injection volume for each sample was 20 μL, and the flow rate was set at 0.8 mL min^{-1}. The detector was set at 60℃ with a gain value of 6.0, and the pressure control was 51 psi. A series of stan-

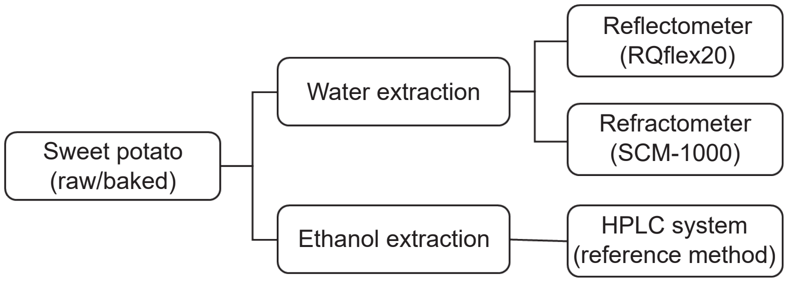

Fig. 1. Explanation diagram for extraction and measurement methods.

dard solutions was prepared by dissolving 10 mg of each sugar (fructose, glucose, sucrose, and maltose) in 1 mL of ultrapure water. These standard solutions were used to create a standard curve.

Reflectometer measurement

The Reflectometer RQflex20 (Merck & Co., Inc., Kenilworth, NJ, USA) was employed in conjunction with sucrose (saccharose) and total sugar (glucose and fructose) test strips, along with the corresponding reagents. The reflectometer was programmed using a bar-coded plastic strip provided with each batch of test strips.

The sucrose test (cat. no. 116141) utilized sucrose phosphorylase to cleave sucrose into fructose and glucose-1-phosphate. Glucose-1-phosphate was then converted by phosphoglucomutase into glucose-6-phosphate, which was subsequently oxidized by nicotinamide adenine dinucleotide (NAD) under the catalytic action of glucose-6-phosphate dehydrogenase to form gluconate-6-phosphate. During this process, the reduced nicotinamide adenine dinucleotide (NADH) produced reduced tetrazolium salt to blue formazan in the presence of diaphorase, which was then measured using the RQflex20. Similarly, in the total sugar test (cat. no. 116136), glucose and fructose were converted to glucose-6-phosphate, oxidized by NAD, and measured using the same method as the sucrose test.

Samples of the water-extracted filtrate were diluted to appropriate concentrations before analysis to ensure they fell within the measurement range. To ensure accuracy and reproducibility, all measurements were performed according to the manufacturer's instructions, including the RQflex20 reflectometer operating manual and user guides for the sucrose and total sugar tests. The measured values were multiplied by the dilution factor, converted accordingly, and presented as % DW (dry weight basis).

Refractometer measurement

This study used a portable digital refractometer (SCM-1000, HM Digital, Carson, CA, USA) with a measurement range of 0–55 degrees Brix to assess the sugar content of sweet potatoes. The measurement was conducted using the water-extracted filtrate, and the resulting values were multiplied by the dilution factor applied during extraction to obtain the final sugar concentration, expressed in degrees Brix (°Bx).

Statistical analysis

To evaluate the performance of the reflectometer and refractometer in measuring sweet potato sugar content, linear regression analyses were conducted using R (version 4.4.1). The sugar content measured by the reference method was the dependent variable, while values measured by the reflectometer and refractometer were used as independent variables. The analyses provided *P*-values, coefficients of determination (R^2), and regression equations for each model, facilitating the assessment of each instrument's performance.

RESULTS AND DISCUSSION

Performance of the reflectometer for determining sugar content in sweet potatoes

To increase the applicability of detection methods, 10 sweet potato cultivars with various tuber flesh colors were selected, including the two predominant varieties, 'Tainung 57' and 'Tainung 66', in Taiwan. Roots were collected at various stages of growth and storage, then divided into raw and baked categories to create samples with varying sugar concentrations. To streamline the extraction process, this study used water as the extraction solvent and eliminated the customary centrifugation step. Specifically, the RQflex20 reflectometer, in conjunction with the Reflectoquant sucrose (saccharose) and total sugar (glucose and fructose) test kits, was employed to analyze the sugar content of sweet potatoes.

Previous research by Lai *et al*. (2013)

found that sucrose was the predominant sugar in raw sweet potatoes, comprising approximately from 49.92 to 92.43% of the total sugar content, depending on the cultivars. This highlights the significance of sucrose content as a key factor influencing sweet potato quality. The detected sucrose content is shown in Fig. 2. Using the RQFlex method, the sucrose content ranged from 1.87 to 23.60% (DW), while the reference method (HPLC) detected a range of 2.00 to 31.84% (DW). The RQFlex data tended to be lower than those obtained from the reference method. The linear relationship between the reference method and the RQFlex method for 93 samples of sucrose content was illustrated. The simple linear regression model was highly significant ($P < 0.001$), with an intercept of -1.56 and a regression coefficient of 1.36. An R^2 of 0.95 indicated a strong relationship between the two methods for measuring sucrose content.

The results for the total sugar (glucose and fructose) test are shown in Fig. 3. Using the RQFlex method, the glucose and fructose content ranged from 0.51 to 7.99% (DW), while the reference method (HPLC) detected a range of 0.48 to 6.57% (DW). A linear regression analysis assessed the relationship between the RQFlex and the reference method for measuring glucose and fructose in 103 samples. The simple linear regression model was highly significant ($P < 0.001$), with an R^2 of 0.86, an intercept of 0.23, and a regression coefficient of 0.82.

Previous studies revealed that raw sweet potatoes contained sucrose, glucose, fructose, and maltose (Lai *et al*. 2013; Huang *et al*. 2014). However, most studies have used the summation of sucrose, glucose, and fructose for analysis (Kays *et al*. 2005; Wei *et al*. 2017; Allan *et al*. 2024). In this research, maltose was not detected in raw sweet potatoes, possibly due to variations in the extraction ratio and differences in the HPLC system configuration used for analysis. Consequently, the combination of water extraction, the RQFlex20 instrument, and sucrose and total sugar (glucose and fructose) tests offered a promising rapid detection method for measuring total sugar content in raw sweet potatoes.

Performance of the refractometer for determining sugar content in sweet potatoes

In modern analytical techniques, efficiency and ease of use are key factors. While the RQFlex20

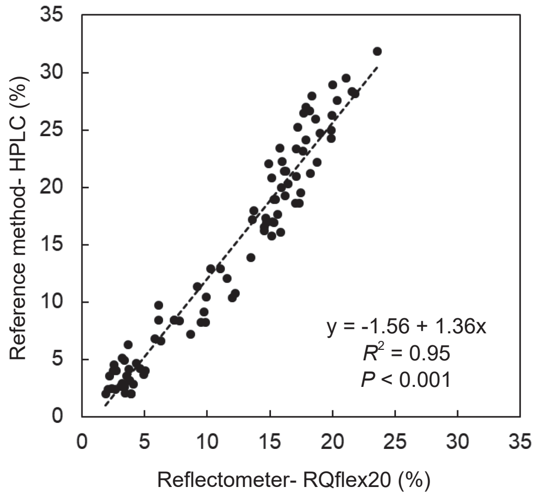

Fig. 2. Linear regression model for sucrose content (dry weight basis) in sweet potatoes analyzed by RQflex20 and high-performance liquid chromatography (HPLC).

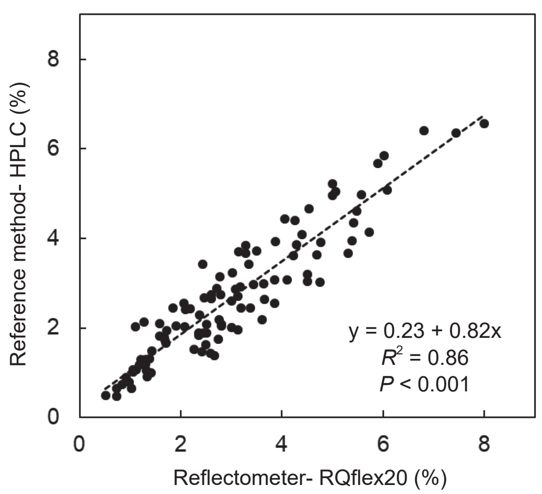

Fig. 3. Linear regression model for glucose and fructose contents (dry weight basis) in sweet potatoes analyzed by RQflex20 and high-performance liquid chromatography (HPLC).

reflectometer requires specialized equipment and a multi-step process, the refractometer provides a more streamlined approach. With a wider measurement range and minimal sample preparation, the refractometer is allowed for direct measurement after extraction, avoiding the time-consuming steps involved in the RQ-Flex method (Jaywant *et al*. 2022).

In this study, the refractometer was used to analyze the soluble sugar content, with measurements expressed in degrees Brix units. The total sugar content obtained by the HPLC method (analyzing sucrose, glucose, and fructose for raw sweet potatoes, and including maltose for baked sweet potatoes) served as a reference for evaluating the applicability of the refractometer method. Sample preparation followed the previous experiment. The results are shown in Fig. 4, with data of reference method expressed on a fresh weight basis for consistency with degrees Brix units. Refractometer measurements ranged from 3.3 to 32.8°Bx, while the reference method (HPLC) detected a range of 0.98 to 20.87% (fresh weight; FW). The refractometer data tended to be higher than those obtained using the reference method. A linear relationship (R^2 = 0.91) was observed between the reference method and the refractometer for measuring total sugar content in 126 samples. The simple linear regression model was highly significant (P < 0.001), with an intercept of -0.39 and a regression coefficient of 0.62. An R^2 of 0.91 indicated a strong relationship between the two methods for measuring total sugar content. Although the refractometer measurements showed some overestimation, consistent with the findings by Buiarelli *et al*. (2016), this method served as a simple and rapid screening tool, with an acceptable margin of error. Since a linear regression model had already been established in this report, it could be used as a calibration tool to correct the overestimation observed in the new method. By using the calibration curve, the refractometer data could be adjusted to more accurately reflect the true values obtained from the reference method, thereby improving measurement precision and minimizing the observed error.

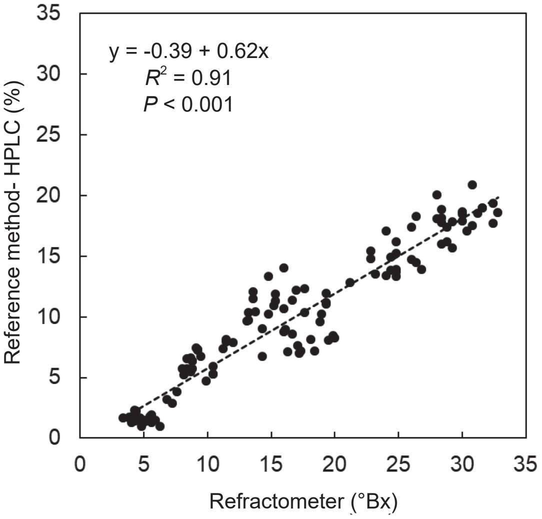

Fig. 4. Linear regression model for total sugar contents (fresh weight basis) in sweet potatoes analyzed by refractometer and high-performance liquid chromatography (HPLC).

The total sugar content significantly increased after baking treatment due to the formation of maltose. This increase primarily occurred because heat activated β-amylase within the sweet potatoes, which catalyzed the conversion of starch into maltose (Laurie *et al*. 2013; Kitahara *et al*. 2017; Nakamura *et al*. 2018; Allan *et al*. 2024). In this study, maltose was detected only in baked sweet potatoes, where it accounted for approximately 23.25 to 86.41% of the total sugars, depending on the cultivar. This study also conducted a regression analysis between the refractometer measurements for baked sweet potatoes and the maltose content measured by the reference method (n = 79) (Fig. 5). The linear regression model was statistically significant (P < 0.001), with an intercept of -4.54 and a regression coefficient of 0.63. The R^2 of 0.90 indicated a strong linear relationship, suggesting that refractometer results could be used to estimate maltose content in baked sweet potatoes. This result was similar to the findings by Nakamura *et al*. (2018), which reported comparable out-

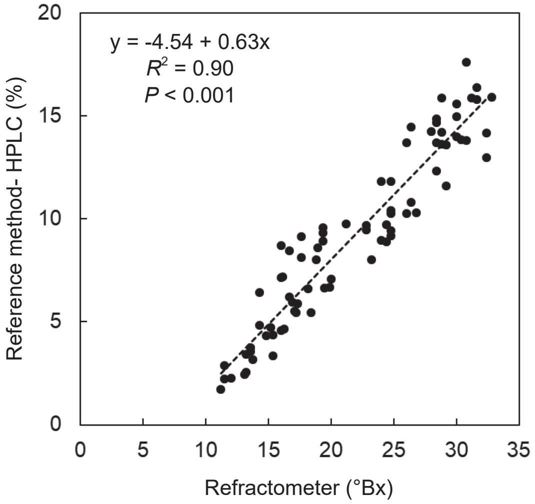

Fig. 5. Linear regression model for predicting maltose content (fresh weight basis) in baked sweet potatoes using the refractometer.

comes. Their research demonstrated that the sweetness of steamed storage roots (n = 221), measured using a refractometer, exhibited a linear correlation with maltose concentrations (%) in the roots of current Japanese cultivars, with a correlation coefficient (r) of 0.855.

While the refractometer had been used previously as a simple method for determining sugar content in sweet potatoes, existing methods primarily involved juicing raw sweet potatoes, with some studies also extracting sugars from steamed sweet potatoes using water (Suárez *et al.* 2016; Šlosár *et al.* 2019; Takahama *et al.* 2021). However, no regression studies had been conducted to establish a correlation between these methods and the HPLC method results. In this study, a water extraction method with a 1 : 3 solid-to-liquid ratio was used to determine the sugar content in sweet potatoes. Filtration through filter paper minimized the influence of suspended solids on the refractometer measurements. Regression analysis confirmed the applicability of this extraction method when it was used with the refractometer, showing that it could be applied to both raw and baked sweet potatoes. The regression equation could be used to convert measurements, yielding even greater accuracy.

CONCLUSION

This study assessed the efficacy of reflectometry and refractometry as rapid methods for analyzing sugar content in sweet potatoes, comparing them to HPLC. Because both methods showed strong linear relationships with HPLC results, refinements to the water extraction process expanded the applicability of these techniques to both raw and baked sweet potatoes, providing a cost-effective, reliable solution for sugar analysis.

REFERENCE

Adu-Kwarteng, E., E. O. Sakyi-Dawson, G. S. Ayernor, V. D. Truong, F. F. Shih, and K. Daigle. 2014. Variability of sugars in staple-type sweet potato (*Ipomoea batatas*) cultivars: The effects of harvest time and storage. Intl. J. Food Prop. 17:410–420. doi:10.1080/10942912.2011.642439

Allan, M. C., S. D. Johanningsmeier, M. Nakitto, O. Guambe, M. Abugu, K. V. Pecota, and G. C. Yencho. 2024. Baked sweetpotato textures and sweetness: An investigation into relationships between physicochemical and cooked attributes. Food Chem. X. 21:101072. doi:10.1016/j.fochx.2023.101072

Buiarelli, F., P. D. Filippo, D. Pomata, C. Riccardi, and D. Rago. 2016. Determination of sugar content in commercial fruit juices by Refractometric, volumetric and chromatographic methods. J. Nutr. Ther. 5:75–84. doi:10.6000/1929-5634.2016.05.03.3

Chan, C. F., C. M. Chiang, Y. C. Lai, C. L. Huang, S. C. Kao, and W. C. Liao. 2014. Changes in sugar composition during baking and their effects on sensory attributes of baked sweet potatoes. J. Food Sci. Technol. 51:4072–4077. doi:10.1007/s13197-012-0900-z

Helgerud, T., S. H. Knutsen, N. K. Afseth, K. F. Stene, E. O. Rukke, and S. Balance. 2016. Evaluation of hand-held instruments for representative determination of glucose in potatoes. Potato Res. 59:99–112. doi:10.1007/s11540-015-9310-8

Huang, C. L., W. C. Liao, C. F. Chan, and Y. C. Lai. 2014. Storage performance of Taiwanese sweet potato cultivars. J. Food Sci. Technol. 51:4019–4025. doi:10.1007/s13197-013-0960-8

Jaywant, S. A., H. Singh, and K. M. Arif. 2022. Sensors and instruments for brix measurement: A review. Sensors 22:2290. doi:10.3390/s22062290

Kays, S. J., Y. Wang, and W. J. McLaurin. 2005. Chemical

and geographical assessment of the sweetness of the cultivated sweetpotato clones of the world. J. Amer. Soc. Hortic. Sci. 130:591–597. doi:10.21273/jashs.130.4.591

Kitahara, K., Y. Nakamura, M. Otani, T. Hamada, O. Nakayachi, and Y. Takahata. 2017. Carbohydrate components in sweetpotato storage roots: Their diversities and genetic improvement. Breed. Sci. 67:62–72. doi:10.1270/jsbbs.16135

Krochmal-Marczak, B., B. Sawicka, B. Krzysztofik, H. Danilčenko, and E. Jariene. 2020. The effects of temperature on the quality and storage stalibity of sweet potato (*Ipomoea batatas* L. [Lam]) grown in Central Europe. Agronomy 10:1665. doi:10.3390/agronomy10111665

Lai, Y. C., C. L. Huang, C. F. Chan, C. Y. Lien, and W. C. Liao. 2013. Studies of sugar composition and starch morphology of baked sweet potatoes (*Ipomoea batatas* (L.) Lam). J. Food Sci. Technol. 50:1193–1199. doi:10.1007/s13197-011-0453-6

Lai, Y. C., S. Y. Wang, H. Y. Gao, K. M. Nguyen, C. H. Nguyen, M. C. Shih, and K. H. Lin. 2016. Physicochemical properties of starches and expression and activity of starch biosynthesis-related genes in sweet potatoes. Food Chem. 199:556–564. doi:10.1016/j.foodchem.2015.12.053

Laurie, S. M., M. Faber, F. J. Calitz, E. I. Moelich, N. Muller, and M. T. Labuschagne. 2013. The use of sensory attributes, sugar content, instrumental data and consumer acceptability in selection of sweet potato varieties. J. Sci. Food Agric. 93:1610–1619. doi:10.1002/jsfa.5932

Nakamura, Y., T. Kuranouchi, A. Ohara-Takada, R. Masuda, T. Kumagai, and K. Katayama. 2018. Maltose generation by beta-amylase and its relation to eating quality of steamed storage roots of sweet potato cultivars, including recently developed varieties in Japan. Jpn. Agric. Res. Q. 52:7–16. doi:10.6090/jarq.52.7

Rees, D., Q. E. A. Van Oirschot, R. Amour, E. Rwiza, R. Kapinga, and T. Carey. 2003. Cultivar variation in keeping quality of sweetpotatoes. Postharvest Biol. Technol. 28:313–325. doi:10.1016/S0925-5214(02)00180-1

Šlosár, M., A. Hegedűsová, O. Hegedűs, I. Mezeyová, J. Farkaš, and M. Golian. 2019. The evaluation of selected qualitative parameters of sweet potato (*Ipomoea batatas* L.) in dependence on its cultivar. Potr. S. J. F. Sci. 13:131–137. doi:10.5219/1036

Suárez, M. H., A. I. M. Hernández, B. R. Galdón, L. H. Rodríguez, C. E. M. Cabrera, D. R. Mesa, ... C. D. Romero. 2016. Application of multidimensional scaling technique to differentiate sweet potato (*Ipomoea batatas* (L.) Lam) cultivars according to their chemical composition. J. Food Compos. Anal. 46:43–49. doi:10.1016/j.jfca.2015.10.008

Takahama, M., T. Noda, R. Ueno, S. Munekata, and H. Araki. 2021. Evaluation of eating quality and starch properties of sweet potato produced in northern Japan. Acta Hortic. 1312:591–598. doi:10.17660/ActaHortic.2021.1312.83

Wei, S., G. Lu, and H. Cao. 2017. Effects of cooking methods on starch and sugar composition of sweetpotato storage roots. PLoS One 12:e0182604. doi:10.1371/journal.pone.0182604

Yoon, H., J. No, W. Kim, and M. Shin. 2018. Textural character of sweet potato root of Korean cultivars in relation to chemical constituents and their properties. Food Sci. Biotechnol. 27:1627–1637. doi:10.1007/s10068-018-0429-7

Yue, F., J. Zhang, J. Xu, T. Niu, X. Lü, and M. Liu. 2022. Effects of monosaccharide composition on quantitative analysis of total sugar content by phenol-sulfuric acid method. Front. Nutr. 9:963318. doi:10.3389/fnut.2022.963318

應用反射光度法及折射光度法於甘藷糖類含量快速檢測之可行性評估

侯惠盈[1] 黃哲倫[2] 葉亦琪[3] 賴永昌[4,*]

摘要

侯惠盈、黃哲倫、葉亦琪、賴永昌。2025。應用反射光度法及折射光度法於甘藷糖類含量快速檢測之可行性評估。台灣農業研究 74(2):151–159。

糖類含量為評估甘藷品質之重要指標，其受品種、成熟度、儲存條件及加工方式等因素而有不同的影響。本研究為開發可替代高效液相層析法 (high-performance liquid chromatography; HPLC) 之快速檢測方法，選用具有不同肉色的 10 種甘藷品種，利用簡化的水萃取法進行糖類萃取，並評估以反射式光度計與折射計檢測生鮮藷與烤藷糖類含量之可行性。試驗以反射式光度計 RQFlex20，搭配檢測試劑組進行分析。其糖類含量與參考方法 (HPLC) 之測值符合直線回歸模式，決定係數 (R^2) 分別為 0.95 (蔗糖) 與 0.86 (葡萄糖與果糖)，顯示此方法具有可應用性。折射計與參考方法亦符合直線回歸模式，R^2 為 0.91，能用以測定總糖 (蔗糖、葡萄糖、果糖及麥芽糖) 含量。另外，使用折射計能進一步預測烤藷中的麥芽糖含量 (R^2 為 0.90)，可克服 RQFlex20 缺乏專用麥芽糖檢測試劑組的限制。本研究應用反射式光度計與折射計，建立快速、經濟且高效檢測甘藷糖類含量的替代方法，有助於農民與加工業者在需要時更快地作出決策。

關鍵詞：甘藷、糖類含量、反射式光度計、折射計。

投稿日期：2024 年 10 月 18 日；接受日期：2024 年 12 月 20 日。

[*] 通訊作者：davidlai489@gmail.com
[1] 農業部農業試驗所嘉義農業試驗分所農藝系助理研究員。臺灣 嘉義市。
[2] 農業部農業試驗所嘉義農業試驗分所農藝系副研究員。臺灣 嘉義市。
[3] 農業部農業試驗所嘉義農業試驗分所農藝系前助理研究員。臺灣 嘉義市。
[4] 農業部農業試驗所嘉義農業試驗分所農藝系研究員兼系主任。臺灣 嘉義市。

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):161–175 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0006

Research Article

Effect of Temperature on the Mycelium Growth and Sporulation of Four Pathotypes of *Pyricularia oryzae* in Taiwan

Yi-Nian Chen[1,*], Dong-Hong Wu[2], Mei-Chun Chen[3], and Pei-Chen Chen[4]

Abstract

Chen, Y. N., D. H. Wu, M. C. Chen, and P. C. Chen. 2025. Effect of temperature on the mycelium growth and sporulation of four pathotypes of *Pyricularia oryzae* in Taiwan. J. Taiwan Agric. Res. 74(2):161–175.

Climate change-related variations in temperature and precipitation may impact the ecology of certain plant pathogens and vectors that are sensitive to changes in humidity and temperature, which could, in turn, affect the incidence and temporal and spatial distribution of plant diseases. Previous research has shown that the rice blast fungus in Taiwan could be divided into 5 pathotype clusters based on virulence to Lijiangxintuanheigu monogenic lines (LTH MLs), with differences in habitat temperatures between these clusters. In this work, we investigated the effect of temperature on mycelial growth and sporulation of different pathotype clusters by analyzing 5 isolates from each of the 4 major clusters. Our findings indicated that the temperature range of 24–32℃ was optimal for the growth and reproduction of rice blast fungus in Taiwan. Among these temperatures, 28℃ was the most favorable. Conditions where the temperature fell below 20℃ or rose above 36℃ significantly restricted the growth and reproduction of the rice blast fungus. All isolates survived, albeit almost completely stopped growing at 36℃. Overall, clusters L4 and L5 exhibited better growth and reproduction at 32℃ compared to 24℃. Conversely, L1 and L2 showed superior growth and reproduction at 24℃ rather than 32℃. L4 had a significantly higher reproductive capacity than the other 3 clusters at 24–32℃. Because of this outcome and the consistent rise in average temperature since 2019, it was believed that temperature was the main cause of L4 and L5 becoming the prevalent clusters in Taiwan. This study clearly illustrated the impact of temperature changes on the epidemic spread of rice blast fungus in Taiwan. It also offered crucial guidance for developing disease-resistant plans for potential climate change scenarios.

Key words: Climate change, Mycelial growth rate, *Pyricularia oryzae*, Sporulation, Temperature.

INTRODUCTION

Climate change might be the greatest threat to conventional agriculture production in Taiwan. As the global temperature increases, the frequency of extreme weather also increases (Mirza 2003), which affects not only crop yields (Song *et al.* 2021) but also host-pathogen interactions (Anderson *et al.* 2004; Viswanath *et al.* 2017). In particular, global temperature increases and water availability changes are expected to cause changes in the suitable areas for crops, which could lead to changes in the distribution of specific crop pathogens (Velásquez *et al.*

Received: October 17, 2024; Accepted: January 23, 2025.
* Corresponding author, e-mail: sogox@tari.gov.tw
1 Assistant Research Fellow, Plant Pathology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
2 Associate Research Fellow, Crop Science Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
3 Project Assistant, Plant Pathology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
4 Professor, Department of Plant Pathology, National Chung Hsing University, Taichung City, Taiwan, ROC.

2018). Temperature, precipitation, and relative humidity (RH) all impact the life cycles of many plant pathogens. Thus, extreme weather events may affect their growth patterns. The distribution of pathogens and endemic diseases is changed as a result (Coakley *et al.* 1999; Harvell *et al.* 2002; Mina & Sinha 2008; Yáñez-López *et al.* 2012; Gautam *et al.* 2013; Bevitori & Ghini 2014). For instance, the first record of a wheat blast outside of South America was discovered in Bangladesh, Asia, in 2016 (Montes *et al.* 2022). The disease is predicted to progressively spread to warm, humid regions surrounding Bangladesh in the future, based on the pathogen's (*Magnaporthe oryzae* pathotype Triticum; MoT) climate adaptation (Mottaleb *et al.* 2018; Montes *et al.* 2022). However, the impact of climate change on plant pathosystems may differ depending on the location (Elad & Pertot 2014).

The host, pathogen, and environmental factors interact in a triangle to form the three most important components of any given plant disease (Velásquez *et al.* 2018). Environmental changes may impact the coevolution of hosts and pathogens (Elad & Pertot 2014). The emergence of a novel and highly pathogenic strain may complicate management approaches (Strange & Scott 2005; Garrett *et al.* 2016). For instance, rising CO_2 concentrations will make wheat more susceptible and *Fusarium graminearum* more virulent (Váry *et al.* 2015). At temperatures above 32℃, *Agrobacterium tumefaciens* loses its ability to infect Kalanchoe due to decreased virulence gene expression (Jin *et al.* 1993). *Cercospora zeae-maydis*, the corn gray leaf spot pathogen, exhibited reduced sporulation and hyphae growth rates when field conditions exceeded 32℃ and 95% RH, thereby reducing the severity of the disease (Paul & Munkvold 2005). However, few studies have looked into the effects of climate change on pathogen population dynamics and changes in disease incidence patterns (Viswanath *et al.* 2017).

Rice, a globally important food crop, is primarily cultivated in tropical and temperate climate regions between 53°N and 40°S latitudes (Koo *et al.* 2013). The warm and humid climate of the cultivation areas favors rice growth and serves as a breeding ground for many pests and diseases. The rice blast pathogen (*Pyricularia oryzae* Cavara) causes severe economic loss in many rice cultivation regions (Ou 1985; Skamnioti & Gurr 2009; Hajano *et al.* 2011). *P. oryzae* thrives at 17–28℃ with high RH, preferring sporulation conditions of 25–29℃, RH > 89%, and leaf dew duration greater than 4 h (Greer & Webster 2001; Viswanath *et al.* 2017; Shahriar *et al.* 2020). Computer model simulations show that temperature is a critical factor affecting pathogen growth, sporulation, and disease progress of the rice blast (Viswanath *et al.* 2017). However, no field experiment has been conducted to prove this assumption. The effects of global temperature change on *P. oryzae* may vary by geographical region. Rising temperatures in cooler subtropical regions increase the likelihood of rice blast epidemics. Nevertheless, a drop in temperature raises the possibility of rice blast epidemics in those warm, humid tropical regions because the present temperatures are already above the disease's ideal range (Luo *et al.* 1998; Ghini *et al.* 2008; Viswanath *et al.* 2017). Field surveys in China since 1970 have confirmed the prediction model proposed by Viswanath *et al.* (2017). Higher spring and early summer temperatures cause a decrease in wheat strip rust disease but an increase in rice blast and wheat Fusarium head blight (Coakley *et al.* 1999). Though the computer model suggests that climate change influences the temporal and spatial distribution of plant diseases, quantitative data on the precise impact of climate change on a specific plant pathogen is still lacking (Bevitori & Ghini 2014).

We found that the five pathotype clusters of *P. oryzae* in Taiwan have distinct habitat temperatures based on the population surveillance of rice blast fungus between 2014 and 2021 (Chen *et al.* 2023b). Interestingly, since 2019, the number of L4 cluster isolates viru-

lent to *Pik* alleles (*Pik*, *Pik-p*, *Pik-m*, *Pik-h*, *Pi1*, *Pi7(t)*) has increased more than 1.7 times compared to previous years. Given that 2019 and 2020 saw exceptionally warm winters in Taiwan, we were curious to know if recent changes in *P. oryzae* field populations in Taiwan were influenced by variations in temperature. In this study, twenty *P. oryzae* isolates belonging to four pathotype clusters were tested for their optimal temperatures for growth and sporulation. The findings demonstrate the distinct temperature preferences of various pathotype cluster isolates. Understanding the factors influencing the growth and sporulation of *P. oryzae* may have important implications for disease management, taking into consideration climate changes and the availability of host-esistant genes.

MATERIALS AND METHODS

P. oryzae isolates

A total of 1,749 *P. oryzae* isolates were gathered from rice fields in Taiwan between 2014 and 2021 (Chen *et al.* 2023b). These isolates were pure cultures originating from a single spore culture (Hayashi *et al.* 2009). Based on their virulence towards Lijiangxintuanheigu monogenic lines (LTH MLs) (S Table 1) (Kobayashi *et al.* 2007), these isolates were categorized into five pathotype clusters (L1–L5). Five isolates from each of the L1, L2, L4, and L5 clusters were randomly chosen for the following experiments (Table 1). Because the L3 cluster is a very small percentage of the population overall, it was excluded from this experiment.

Table 1. Pathotype clusters of 20 *Pyricularia oryzae* isolates used in this study (Chen *et al.* 2023b)

Pathotype cluster	Target gene[z]	Isolate[y]	Collection date	Location
L1	*Pish*	DAL2a3-1605	May, 2016	Dalin, Chiayi
		HL5a2-1606	Jun, 2016	Houli, Taichung
		CT2a1(1)-1803	Mar, 2018	Caotun, Nantou
		MN1a2-1803	Mar, 2018	Meinong, Kaohsiung
		MN6a3-1908	Aug, 2019	Meinong, Kaohsiung
L2	*Pita*	JX2a1-1405	May, 2014	Jiaoxi, Yilan
		SHC1a3-1504	Apr, 2015	Qingshui, Taichung
		LN2b3-1605	May, 2016	Linnei, Yunlin
		MN4a2-1804	Apr, 2018	Meinong, Kaohsiung
		LY3a1-1805	May, 2018	Luye, Taitung
L4	*Pik*, *Pik-p*, *Pik-m*, *Pik-h*, *Pi1*, *Pi7(t)*, *Pish*, *Pita*, *Pi19(t)*	EM1a1-1903	Mar, 2019	Emei, Hsinchu
		LJ3a2-1903	Mar, 2019	Liujia, Tainan
		SX3a1-1905	May, 2019	Sanxing, Yilan
		HW2a1-2003	Mar, 2020	Huwei, Yunlin
		LL1a1-2004	Apr, 2020	Linluo, Pingtung
L5	*Piz-t*	KD2a1-1901	Jan, 2019	Kanding, Pingtung
		GS3a1-1903	Mar, 2019	Guanshan, Taitung
		GOGU3a2-1905	May, 2019	Gongguan, Miaoli
		SF5a3-1905	May, 2019	Shoufeng, Hualien
		TL3a1-1905	May, 2019	Tongluo, Miaoli

[z] The target gene means the pathotype cluster compatible (virulent) to these genes.
[y] The number after the "-" represents the year and month of collection.

Mycelial growth test

Fungal isolates from stock cultures were revived on a 9 cm potato dextrose agar (PDA) plate (Bacto, Mt Pritchard, Australia). After the mycelium had completely covered the plate, a 5 mm mycelium disc was taken from the edge and placed in the center of a new PDA plate. Plates were incubated at 12, 16, 20, 24, 28, 32, 36, and 40℃ for 5 d in darkness. The average daily growth rate of the fungal colony was computed by measuring its diameters. All mycelial disc culture plates subjected to temperature treatments were subsequently incubated at room temperature for another two wk to monitor pathogen viability and growth potential. After the two-week observation period, cultures were examined under a microscope. The absence of visible hyphal growth was used as the criterion to confirm pathogen mortality. The experiment was conducted twice, with three replicates of each treatment.

Sporulation test

Fungal isolates were revived on a V-8 juice agar (each liter containing V-8 juice 100 mL, $CaCO_3$ 0.2 g, agar 17 g, pH 6.5) plate and then augmented with the liquid spawn method by Chen *et al.* (2021b). The mycelial pellets were homogenized with the prune broth medium (each liter containing prune 15 g, starch 2.5 g, yeast extract 0.5 g, pH 6.5) using a homogenizer (Oster Blender 6640-022, Oster, Chicago, IL, USA). One mL of the resulting suspension was spread on 5.5 cm OFA plates (oat flour 10 g L^{-1}, agar 20 g L^{-1}), and the excess moisture was air-dried. The plates were then incubated for 4 d at 12, 16, 20, 24, 28, 32, 36, and 40℃. All chambers were set with 12 h under blacklight blue (PULSAR, F40T8/BLB) and 12 h darkness. Spores were collected by adding 5 mL of 0.02% Tween 80 and gently scrapping with a glass slide. The quantity of spores was measured using a hemocytometer (Hausser Scientific, Horsham, PA, USA) after spore suspensions were filtered through a layer of Miracloth (EMD Millipore, Billerica, MA, USA). The experiment was conducted twice, with four replicates per treatment in each trial.

Statistical analyses

In the mycelial growth test and sporulation test, the experiments aimed to evaluate the growth responses of isolates under the effects of different variable sources, including the isolates, temperature treatments, and their interactions. Statistical analysis was conducted through an analysis of variance (ANOVA) for these three factors. The 20 isolates were derived from four distinct pathotype clusters, allowing the factor of pathotype clusters to be further partitioned into variations between clusters and within-cluster isolates. When significant differences were detected in the ANOVA for any factor, Fisher's protected least significant difference (PLSD) test was applied for pairwise comparisons among treatment combinations. Differences were considered significant at the 5% level and were denoted using distinct letters. Statistical analysis was performed by the R package, Agricolae (Version 3.6.0) (de Mendiburu 2015) via ANOVA followed by Fisher's least square difference (LSD) test at a $P < 0.05$ significance level. The data was displayed as the mean ± standard deviation derived from a minimum of three duplicates.

RESULTS

Determination of optimal growth temperatures for four pathotype clusters

The blast isolates were categorized into four major pathotype clusters based on their pathogenic reactions (Table 1). L4 cluster showed pathogenic to rice cultivars carrying the *Pik* alleles (*Pik*, *Pik-p*, *Pik-m*, *Pik-h*, *Pi1*, and *Pi7*), *Pish*, *Pita*, and *Pi19(t)*. L1 cluster showed pathogenic to those carrying the *Pish* gene and L5 cluster showed pathogenic to the rice cultivars carrying the *Piz-t* gene (Chen *et al.* 2023b). ANOVA was performed on the data to compare how temperature affected the mycelial growth rates of various

pathotype cluster isolates of the rice blast fungus in Taiwan. The 20 isolates were derived from four distinct pathotype clusters, allowing the factor of pathotype clusters to be further partitioned into variations between clusters and within-cluster isolates. The findings (Table 2) demonstrated that the two primary factors of temperature and isolate had a significant impact ($P < 0.001$) on the mycelial growth rate of the rice blast fungus, but the primary factor of pathotype clusters did not show a significant difference ($P > 0.05$). Additionally, significant interactions were observed ($P < 0.001$) between temperature and pathotype cluster and between temperature and isolate. It suggests that distinct pathotype clusters and isolates each had a favored temperature for mycelium growth. Among these factors, temperature had the greatest impact on the mycelial growth rate.

The results showed that 28℃ was the optimal mycelium growth temperature for *P. oryzae*, with an average rate of 2.93 mm day^{-1}. Mycelium growth rates at 32 and 24℃ were 2.56 mm and 2.48 mm day^{-1}, respectively (Fig. 1). Most isolates did not grow but remained viable when incubated at 36℃. All test isolates stopped growing and some even perished at 40℃. The isolate KD2al-1901 had the highest growth rate (an average of 1.49 mm day^{-1} under all temperature treatments), and isolate GOGU3a2-1905 was the slowest (an average of 1.19 mm day^{-1}) (Table 3).

The mycelial growth of four pathotype clusters at different temperatures revealed that 28℃ was the optimal temperature for each cluster. The L5 cluster demonstrated a notably greater growth rate at 32℃ in comparison to 24℃, while the other three pathotype clusters did not exhibit any notable variations when cultivated at either 24 or 32℃ (S Table 2).

Effect of temperature on the sporulation of *P. oryzae* pathotypes

The 20 isolates were derived from four distinct pathotype clusters, allowing the factor

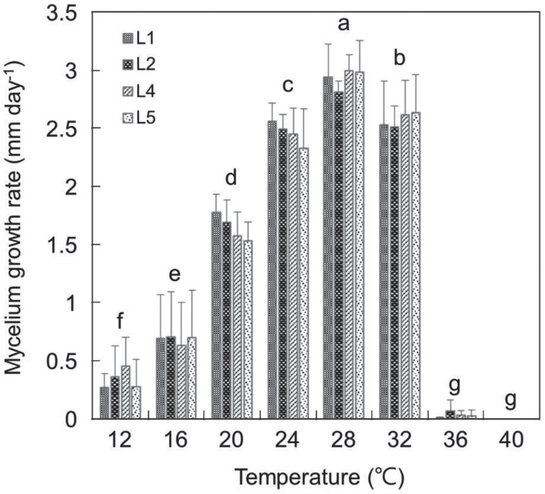

Fig. 1. The average daily mycelium growth rate (mm day^{-1}) of four pathotype clusters of rice blast fungus cultured on potato dextrose agar medium under different temperatures. Error bars represent the standard errors of the mean values of 5 isolates within the cluster. The same lowercase letters above the gray bars indicate that the mean values are not significantly different at $P < 0.05$ among the temperature subgroup.

Table 2. Effects of different incubation temperatures on the mycelium growth rate (mm day^{-1}) of 20 *Pyricularia oryzae* isolates based on analysis of variance (ANOVA).

Treatment	*df*	*MS*	*F*
Temperature	7	88.64	590.933***
Isolate	19		
Among pathotype	(3)	0.05	0.278
Within isolate	(16)	0.18	17.999***
Temperature × pathotype	21	0.07	6.731***
Temperature × isolate	112	0.15	15.129***
Error	320	0.01	

*, **, and *** indicate significant differences at $P < 0.05$, $P < 0.01$, and $P < 0.001$. The mean value of each isolate represents three replicates.

Table 3. Average daily mycelium growth rate (mm day^{-1}) of 20 isolates of *Pyricularia oryzae* in four pathotype clusters.

Isolate	Pathotype cluster	Mycelium growth rate (mm day^{-1})
DAL2a3-1605	L1	1.37[z] cdef[y]
HL5a2-1606		1.46 ab
CT2a1(1)-1803		1.28 hij
MN1a2-1803		1.38 cde
MN6a3-1908		1.24 ijk
Subgroup mean of L1		1.346
JX2a1-1405	L2	1.35 defg
SHC1a3-1504		1.41 bc
LN2b3-1605		1.24 ijk
MN4a2-1804		1.36 cdef
LY3a1-1805		1.29 ghi
Subgroup mean of L2		1.33
EM1a1-1903	L4	1.41 bcd
LJ3a2-1903		1.44 ab
SX3a1-1905		1.33 efgh
HW2a1-2003		1.36 cdef
LL1a1-2004		1.25 ij
Subgroup mean of L4		1.358
KD2a1-1901	L5	1.49 a
GS3a1-1903		1.33 efgh
GOGU3a2-1905		1.19 k
SF5a3-1905		1.23 jk
TL3a1-1905		1.31 fgh
Subgroup mean of L5	1.31	

[z] The mean value of each isolate represents four replicates.

[y] Values are expressed as the mean of each isolate, and means within a column followed by the same letter(s) are not significantly different at the 5% level as determined by Fisher's protected least significant difference (PLSD) test.

of pathotype clusters to be further partitioned into variations between clusters and within-cluster isolates. The effects of different incubation temperatures on the sporulation of the *P. oryzae* isolates tested by ANOVA showed significant differences ($P < 0.001$) (Table 4). There were also significant differences between isolates but not in pathotypes. Significant differences were observed in the interactions between temperature and pathotype and temperature and isolate as well. The findings showed that distinct pathotypes and isolates had preferred sporulation temperatures.

For *P. oryzae*, the optimal sporulation temperature was 28℃, with an average of 16.6 × 10^5 conidia $plate^{-1}$ produced. The average sporulation at 24℃ and 32℃ was 13.8 × 10^5 conidia $plate^{-1}$ and 12.7 × 10^5 conidia $plate^{-1}$, respectively. All isolates failed to sporulate when incubated at 40℃ (Fig. 2). Isolate SX3a1-1905 exhibited the highest sporulation of all the tested isolates, with an average of 17.9 × 10^5 conidia $plate^{-1}$ calculated from all the sporulation data at all temperatures (Table 5). Isolate LN2b3-1605 had the lowest sporulation, with an average of 0.2 × 10^5 conidia $plate^{-1}$. Across pathotypes, the optimal sporulation temperature for the L4 cluster was 28℃, resulting in an average

Table 4. Analysis of variance (ANOVA) result of the effects of different incubation temperatures on the sporulation of 20 rice blast isolates in four pathotype clusters.

Treatment	*df*	*MS*	*F*
Temperature	7	3.842e + 13	16.96***
Isolate	19		
Among pathotype	(3)	1.743e + 13	2.02
Within Isolate	(16)	8.630e + 12	79.76***
Temperature × pathotype	21	4.947e + 12	45.73***
Temperature × isolate	112	2.265e + 12	20.94***
Error	480	1.082e + 11	

*, **, and *** indicate significant differences at $P < 0.05$, $P < 0.01$, and $P < 0.001$. The mean value of each isolate represents four replicates.

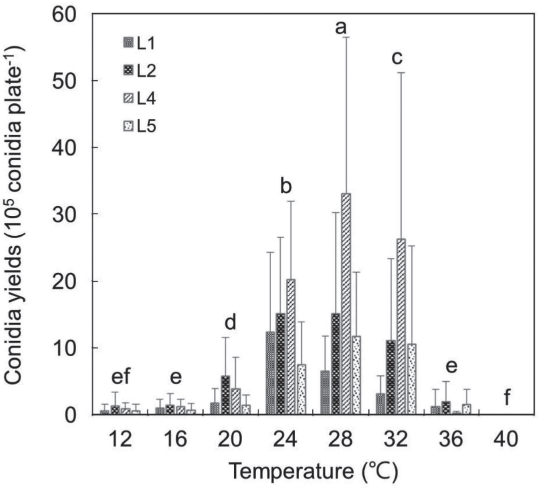

Fig. 2. The average conidia yields (conidia plate^{-1}) of four rice blast fungus pathotype clusters cultured on the OFA medium under different temperatures. Error bars represent the standard errors of the mean values of 5 isolates within the cluster. The same lowercase letters above the gray bars indicate that the mean values are not significantly different at $P < 0.05$ among the temperature subgroup.

of 33.1 × 10^5 conidia plate^{-1}. At 32℃, the L4 cluster generated 26.2 × 10^5 conidia plate^{-1}. For the L1 cluster, 24℃ was the ideal sporulation temperature that sporulated an average of 15.1 × 10^5 conidia plate^{-1}. The optimal sporulation temperature for L5 cluster isolates was 28–32℃ at which an average of 10.5–11.7 × 10^5 conidia plate^{-1} was produced. The L2 cluster generated the highest number of conidia at 24–28℃ with an average of 15.1 × 10^5 conidia plate^{-1} (S Table 2).

DISCUSSION

Global warming alters not only the optimal crop cultivation regions but also the growth and distribution of plant pathogens and pests (Velásquez *et al.* 2018). Taiwan experienced a relatively warm winter in 2019, with average temperatures of 2–4℃ higher from January and February than previous decades (Chen *et al.* 2023a). This abnormally high temperature caused the rice blast to occur earlier, in mid-March rather than April (Chen *et al.* 2021a). As more isolates of the L4 cluster were collected from the field yearly between 2018 and 2020, the L4 cluster of *P. oryzae* began to predominate. In contrast, between 2014 and 2018, the percentages of L1 and L2 cluster isolates declined yearly (Chen *et al.* 2023b). The disease triangle showed that both the host and environment can influence the evolution and adaptation of pathogens. Since the Tainan 11 cultivar was the dominant cultivated rice in Taiwan from 2014 to 2021 with no notable changes, it is hypothesized that the dramatic changes in rice blast fungus pathotypes over the last eight years were related to temperature variations.

According to our results, temperature and isolation, were the two main factors affecting the mycelium growth and sporulation of *P. oryzae*. However, the effect of the pathotype was not substantial. This suggests that the mycelial growth rate and sporulation of the rice

Table 5. Average spore yields of twenty rice blast isolates in four pathotype clusters

Isolate	Pathotype cluster	No. of conidia per plate	
DAL2a3-1605	L1	128,063[z]	ij[y]
HL5a2-1606		838,000	d
CT2a1(1)-1803		222,938	ghi
MN1a2-1803		307,125	fgh
MN6a3-1908		154,531	hij
Subgroup mean of L1		330,131	
JX2a1-1405	L2	502,188	e
SHC1a3-1504		693,813	d
LN2b3-1605		20,094	j
MN4a2-1804		1,599,063	b
LY3a1-1805		411,656	ef
Subgroup mean of L2		645,363	
EM1a1-1903	L4	1,697,219	ab
LJ3a2-1903		1,001,688	c
SX3a1-1905		1,788,219	a
HW2a1-2003		812,813	d
LL1a1-2004		49,469	j
Subgroup mean of L4		1,069,882	
KD2a1-1901	L5	329,750	fg
GS3a1-1903		1,049,094	c
GOGU3a2-1905		418,969	ef
SF5a3-1905		267,438	fghi
TL3a1-1905		37,000	j
Subgroup mean of L5		420,450	

[z] The mean value of each isolate represents four replicates.
[y] Values are expressed as the mean of each isolate, and means within a column followed by the same letter(s) are not significantly different at the 5% level as determined by Fisher's protected least significant difference (PLSD) test.

blast fungus vary with temperature and differ between isolates. Nonetheless, due to individual differences in mycelial growth rate and sporulation of isolates within each cluster, the differences among the clusters were insignificant. Furthermore, the interactions of temperature with pathotype and temperature with isolate also had a notable impact on the mycelial growth rate and sporulation of the rice blast fungus. This indicates that the mycelial growth rate and sporulation of the isolates and pathotypes vary with temperature changes.

Our findings indicated that 24–32℃ is the ideal temperature range for the growth and reproduction of the rice blast fungus in Taiwan. The growth and reproduction of the fungus are severely limited when the temperature drops below 20℃ or rises above 36℃. The rice blast fungus in Taiwan grew most favorably at 28℃, achieving mycelial growth of 2.93 mm day^{-1} and sporulation of 16.67 × 10^{5} conidia plate^{-1}. While sporulation was higher at 24℃ (13.8 × 10^{5} conidia plate^{-1}) than at 32℃ (12.7 × 10^{5} conidia plate^{-1}), mycelial growth rate was faster at 32℃ (2.57 mm day^{-1}) than at 24℃ (2.46 mm day^{-1}). Furthermore, Taiwan rice blast fungus tolerated temperatures up to 36℃, although growth and reproduction were inhibited in these conditions. The average high temperature on Taiwan's flatlands during the first rice crop season, which runs from

January to June, ranges between 20.9℃ and 31.1℃. During the second crop season, from July through November, temperatures typically range from 22.3 to 32.3℃ (data source: https://www.cwa.gov.tw/V8/C/C/Statistics/monthlymean.html). The findings of this experiment, which showed that temperatures above 32℃ were unfavorable for the growth and reproduction of rice blast fungus, precisely explained why rice blast disease occurred more frequently in Taiwan during the relatively cooler first crop season and less frequently during the warmer second season.

For all pathotype clusters, the ideal temperature for mycelial growth was 28℃. Clusters L4 (2.62 mm day^{-1}) and L5 (2.63 mm day^{-1}) exhibited faster mycelial growth rates at 32℃ than do L1 (2.53 mm day^{-1}) and L2 (2.51 mm day^{-1}). In contrast, clusters L1 (2.56 mm day^{-1}) and L2 (2.49 mm day^{-1}) exhibited faster mycelial growth rates at 24℃ than do clusters L4 (2.45 mm day^{-1}) and L5 (2.33 mm day^{-1}). Results showed that mycelial growth and development of clusters L4 and L5 were favored by warmer conditions (32℃), while clusters L1 and L2 were favored by cooler conditions (24℃). The ideal temperatures for sporulation differed slightly between the clusters. The L1 cluster had an ideal temperature of 24℃ (12.4×10^5 conidia $plate^{-1}$); the L2 cluster had an optimal temperature of 24 to 28℃ (both producing 15.1×10^5 conidia $plate^{-1}$); the L4 cluster had an optimal temperature of 28℃ (33.1×10^5 conidia $plate^{-1}$); and the L5 cluster had an optimal temperature of 28 to 32℃ ($11.7–10.5 \times 10^5$ conidia $plate^{-1}$) (S Table 2). The findings indicate that sporulation in clusters L4 and L5 is more advantageous under warmer conditions (32℃), while clusters L1 and L2 benefit from cooler conditions. The highly virulent L4 cluster exhibited significantly higher sporulation levels between 24–32℃ compared to the other three clusters. This indicates that L4 has a greater potential for infection within this temperature range than the other clusters. The L2 cluster was the least virulent of all the clusters, even though it showed more sporulation between 24℃ and 32℃ than the L5 cluster. Consequently, within this temperature range, L2 was not conducive to effective infection and development on the host rice plants. The above results imply that warmer conditions (32℃) will support the survival and growth of clusters L4 and L5. On the other hand, clusters L1 and L2 will grow and develop more readily in colder environments (24℃). The results may explain why L4 cluster was dominant from all *P. oryzae* isolates collected in 2019 and 2020 when the average temperature in Spring were much higher than the previous years.

The L1 and L5 clusters had the widest range of average temperatures in their distribution areas (both 11.9–30.7℃), according to an analysis of temperature data from the habitats of the five pathotype clusters (Chen *et al.* 2023b). In terms of average maximum temperature, cluster L2 had an average of 28.5℃, while clusters L1, L4, and L5 in all distribution areas had an average above 29.3℃. The mean of the lowest temperatures in the distribution areas of clusters L1, L4, and L5 was higher than 22.7℃, while the mean for cluster L2 was 21.9℃. It is inferred that an environmental temperature above 29℃ promotes the survival of clusters L1, L4, and L5, based on the habitat temperature data of pathotype clusters. Conversely, the L2 cluster has a better chance of surviving in an environment with a temperature below 22.6℃. Taking into account the growth and sporulation abilities of pathotype clusters at various temperatures, as well as their adaptability to environmental temperatures, we can reasonably conclude that when the environmental temperature exceeds 29℃, only clusters L4 and L5 will have a competitive advantage, whereas cluster L1 may lose competitiveness due to a significant decline in sporulation ability. Even though the daytime high may be higher than 29℃, if the nighttime low stays at or below 24℃, there is a chance that this will positively impact L1 cluster development. Conversely, the L2 cluster may instead gain a competitive advantage when the environment temperature falls below 23℃. However, it remains unclear what causes such differences in temperature adaptability between the four patho-

type clusters, and further research is needed to clarify this.

Other plant pathogens have also been reported to have different optimal growth temperatures among isolates. For example, *Phytophthora infestans* isolates from Europe and the Mediterranean have different temperature preferences in different stages of the life cycle, such as the latent infection period, sporulation, and sporangia production (Mariette *et al.* 2016). The outbreak of the wheat tripe rust disease in eastern USA and Australia since 2000 is largely due to the increase of a new *Puccinia striiformis* f. sp. *tritici* isolate that is capable of producing more conidia at higher temperatures (Hovmøller *et al.* 2008; Garrett *et al.* 2009; Milus *et al.* 2009). These examples illustrated that temperature plays a selective role in favoring fungal isolates with the highest fitness to become a dominant population in a short time. Global warming favors *P. oryzae* isolates that sporulate and grow faster at high temperatures. We speculate that the L4 cluster might become the predominant pathotype in Taiwan if the same rice cultivars are continually planted.

Under the influence of global warming, temperature rise and water availability changes are expected to be important factors affecting the future distribution areas of crop production, disease vectors, and pathogen populations (Velásquez *et al.* 2018). Among them, the impact of temperature changes on pests and plant diseases is the most critical (Garrett *et al.* 2022). Some studies have pointed out that a higher temperature might suppress the development of rice blast disease in the fields (Bevitori & Ghini 2014). However, in this study, we have found that partial *P. oryzae* could survive at higher temperatures, and these heat-adapted pathogens may become more prevalent in a warmer climate because of their shorter life cycles and sporulation of more conidia. Short life history and high spore yield are conducive to accelerating the evolution of fungal pathogens to produce new virulent strains with better adaptability, thereby changing the pathogen population structure and disease ecology (Velásquez *et al.* 2018). *P. oryzae* had been proven to be a fast-coevolving pathogen with the rice host (Kanzaki *et al.* 2012; Li *et al.* 2019). No experimental evidence has shown that environmental factors could speed up their evolutionary dynamics. Long-term monitoring and data collection are needed to verify the effect of climate changes on plant disease epidemics (Jeger & Pautasso 2008; Garrett *et al.* 2016). This study showed that pathotypes of *P. oryzae* collected from 2014 to 2021 had different optimal temperatures for growth and sporulation. More factors should be evaluated to obtain a better prediction and monitoring model that can help us to make better decisions for disease management in the future.

REFERENCES

Anderson, P. K., A. A. Cunningham, N. G. Patel, F. J. Morales, P. R. Epstein, and P. Daszak. 2004. Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. Trends Ecol. Evol. 19:535–544. doi:10.1016/j.tree.2004.07.021

Bevitori, R. and R. Ghini. 2014. Rice blast disease in climate change times. J. Rice Res. 3:e111. doi:10.4172/2375-4338.1000e111

Chen, Y. N., M. C. Chen, and P. C. Chen. 2021a. Pathogen diversity and inoculum source of rice blast disease in Taiwan. p.87–98. *in*: Applicable Solution Against Rice Blast in Asia. (Fukuta, Y., A. Hasebe, M. Kato, and R. Y. Yang, eds.) Food and Fertilizer Technology Center for the Asian and Pacific. Taipei, Taiwan. 226 pp.

Chen, Y. N., D. H. Wu, M. C. Chen, and P. C. Chen. 2021b. A simple and economical method to induce sporulation of *Pyricularia oryzae*. J. Taiwan Agric. Res. 70:1–12. doi:10.6156/JTAR.202103_70(1).0001

Chen, Y. N., M. H. Lai, and J. H. Ou. 2023a. Adaptation strategies and measures in Taiwan in response to ecological changes in rice blast caused by climate change. p.47–56. *in*: Proceedings of symposium on application of plant protection technology in resilient agriculture. November 10, 2023. Taichung, Taiwan. The Plant Protection Society of Republic of China. Taichung, Taiwan. (in Chinese with English abstract)

Chen, Y. N., D. H. Wu, M. C. Chen, M. T. Hsieh, W. S. Jwo, G. C. Lin, ... P. C. Chen. 2023b. Dynamics of spatial and temporal population structure of *Pyricularia oryzae* in Taiwan. Pest Manage. Sci. 79:4254–

4263. doi:10.1002/ps.7621

Coakley, S. M., H. Scherm, and S. Chakraborty. 1999. Climate change and plant disease management. Annu. Rev. Phytopathol. 37:399–426. doi:10.1146/annurev.phyto.37.1.399

de Mendiburu, F. 2015. Agricolae: Statistical procedures for agricultural research. R Package Version 1.2-3. http://CRAN.R-project.org/package=agricolae (visit on 12/5/2022)

Elad, Y. and I. Pertot. 2014. Climate change impacts on plant pathogens and plant diseases. J. Crop Improv. 28:99–139. doi:10.1080/15427528.2014.865412

Garrett, K. A., D. P. Bebber, B. A. Etherton, K. M. Gold, A. I. P. Sulá, and M. G. Selvaraj. 2022. Climate change effects on pathogen emergence: Artificial intelligence to translate big data for mitigation. Annu. Rev. Phytopathol. 60:357–378. doi:10.1146/annurev-phyto-021021-042636

Garrett, K. A., M. Nita, E. D. De Wolf, P. D. Esker, L. Gomez-Montano, and A. H. Sparks. 2016. Plant pathogens as indicators of climate change. p.325–338. *in*: Climate Change. 2nd ed. (Letcher, T. M., ed.) Elsevier, Boston. 608 pp.

Garrett, K. A., M. Nita, E. D. De Wolf, L. Gomez, and A. H. Sparks. 2009. Plant pathogens as indicators of climate change. p.425–437. *in*: Climate and Global Change: Observed Impacts on Planet Earth. (Letcher, T. M., ed.) Elsevier, Oxford. 444 pp.

Gautam, H. R., M. L. Bhardwaj, and R. Kumar. 2013. Climate change and its impact on plant diseases. Curr. Sci. 105:1685–1691.

Ghini, R., E. Hamada, and W. Bettiol. 2008. Climate change and plant diseases. Sci. Agric. 65:98–107. doi:10.1590/S0103-90162008000700015

Greer, C. A. and R. K. Webster. 2001. Occurrence, distribution, epidemiology, cultivar reaction, and management of rice blast disease in California. Plant Dis. 85:1096–1102. doi:10.1094/pdis.2001.85.10.1096

Hajano, J. U. d., M. A. Pathan, Q. A. Rajput, and M. A. Lodhi. 2011. Rice blast-mycoflora, symptomatology and pathogenicity. IJAVMS 5:53–63. doi:10.5455/ijavms.20110226124750

Harvell, C. D., C. E. Mitchell, J. R. Ward, S. Altizer, A. P. Dobson, R. S. Ostfeld, and M. D. Samuel. 2002. Climate warming and disease risks for terrestrial and marine biota. Science 296:2158–2162. doi:10.1126/science.1063699

Hayashi, N., N. Kobayashi, C. M. V. Cruz, and Y. Fukuta. 2009. Protocols for the sampling of diseased specimens and evaluation of blast disease in rice. p.17–33. *in*: JIRCAS Working Report No. 63. (Fukuta, Y., C. M. V. Cruz, and N. Kobayashi, eds.) Japan International Research Center for Agricultural Sciences. Tsukuba, Japan. 124 pp.

Hovmøller, M. S., A. H. Yahyaoui, E. A. Milus, and A. F. Justesen. 2008. Rapid global spread of two aggressive strains of a wheat rust fungus. Mol. Ecol. 17:3818–3826. doi:10.1111/j.1365-294X.2008.03886.x

Jeger, M. J. and M. Pautasso. 2008. Plant disease and global change: The importance of long-term data sets. New Phytol. 177:8–11. doi:10.1111/j.1469-8137.2007.02312.x

Jin, S., Y. N. Song, W. Y. Deng, M. P. Gordon, and E. W. Nester. 1993. The regulatory VirA protein of *Agrobacterium tumefaciens* does not function at elevated temperatures. J. Bacteriol. 175:6830–6835. doi:10.1128/jb.175.21.6830-6835.1993

Kanzaki, H., K. Yoshida, H. Saitoh, K. Fujisaki, A. Hirabuchi, L. Alaux, ... R. Terauchi. 2012. Arms race co-evolution of *Magnaporthe oryzae AVR-Pik* and rice *Pik* genes driven by their physical interactions. Plant J. 72:894–907. doi:10.1111/j.1365-313X.2012.05110.x

Kobayashi, N., M. J. Telebanco-Yanoria, H. Tsunematsu, H. Kato, T. Imbe, and Y. Fukuta. 2007. Development of new sets of international standard differential varieties for blast resistance in rice (*Oryza sativa* L.). Jpn. Agric. Res. Q. 41:31–37. doi:10.6090/jarq.41.31

Koo, B. H., S. C. Yoo, J. W. Park, C. T. Kwon, B. D. Lee, G. An, ... N. C. Paek. 2013. Natural variation in *OsPRR37* regulates heading date and contributes to rice cultivation at a wide range of latitudes. Mol. Plant 6:1877–1888. doi:10.1093/mp/sst088

Li, J., Q. Wang, C. Li, Y. Bi, X. Fu, and R. Wang. 2019. Novel haplotypes and networks of *AVR-Pik* alleles in *Magnaporthe oryzae*. BMC Plant Biol. 19:204. doi:10.1186/s12870-019-1817-8

Luo, Y., P. S. Teng, N. G. Fabellar, and D. O. TeBeest. 1998. The effects of global temperature change on rice leaf blast epidemics: A simulation study in three agroecological zones. Agric. Ecosyst. Environ. 68:187–196. doi:10.1016/S0167-8809(97)00082-0

Mariette, N., A. Androdias, R. Mabon, R. Corbière, B. Marquer, J. Montarry, and D. Andrivon. 2016. Local adaptation to temperature in populations and clonal lineages of the Irish potato famine pathogen *Phytophthora infestans*. Ecol. Evol. 6:6320–6331. doi:10.1002/ece3.2282

Milus, E. A., K. Kristensen, and M. S. Hovmøller. 2009. Evidence for increased aggressiveness in a recent widespread strain of *Puccinia striiformis* f. sp. *tritici* causing stripe rust of wheat. Phytopathology 99:89–94. doi:10.1094/phyto-99-1-0089

Mina, U. and P. Sinha. 2008. Effects of climate change on plant pathogens. EnviroNews 14:6–10.

Mirza, M. M. Q. 2003. Climate change and extreme weather events: Can developing countries adapt? Clim. Policy 3:233–248. doi:10.3763/cpol.2003.0330

Montes, C., S. G. Hussain, and T. J. Krupnik. 2022. Variable climate suitability for wheat blast (*Magnaporthe oryzae* pathotype Triticum) in Asia: Results from a continental-scale modeling approach. Int. J. Biometeorol. 66:2237–2249. doi:10.1007/s00484-022-02352-9

Mottaleb, K. A., P. K. Singh, K. Sonder, G. Kruseman, T. P. Tiwari, N. C. D. Barma, ... O. Erenstein. 2018. Threat of wheat blast to South Asia's food security: An ex-ante analysis. PLoS One 13:e0197555. doi:10.1371/journal.pone.0197555

Ou, S. H. 1985. Rice Diseases. 2nd ed. Commonwealth Mycological Institute. Kew, UK. 380 pp.

Paul, P. A. and G. P. Munkvold. 2005. Influence of temperature and relative humidity on sporulation of *Cercospora zeae-maydis* and expansion of gray leaf spot lesions on maize leaves. Plant Dis. 89:624–630. doi:10.1094/pd-89-0624

Shahriar, S. A., A. A. Imtiaz, M. B. Hossain, A. Husna, and M. N. K. Eaty. 2020. Review: Rice blast disease. ARRB 35:50–64. doi:10.9734/arrb/2020/v35i130180

Skamnioti, P. and S. J. Gurr. 2009. Against the grain: Safeguarding rice from rice blast disease. Trends Biotechnol. 27:141–150. doi:10.1016/j.tibtech.2008.12.002

Song, J. S., J. H. Im, Y. H. Park, S. H. Lim, M. J. Yook, B. W. Lee, ... D. S. Kim. 2021. Modeling the effects of elevated temperature and weed interference on rice grain yield. Front. Plant Sci. 12:663779. doi:10.3389/fpls.2021.663779

Strange, R. N. and P. R. Scott. 2005. Plant disease: A threat to global food security. Annu. Rev. Phytopathol. 43:83–116. doi:10.1146/annurev.phyto.43.113004.133839

Váry, Z., E. Mullins, J. C. McElwain, and F. M. Doohan. 2015. The severity of wheat diseases increases when plants and pathogens are acclimatized to elevated carbon dioxide. Glob. Change Biol. 21:2661–2669. doi:10.1111/gcb.12899

Velásquez, A. C., C. D. M. Castroverde, and S. Y. He. 2018. Plant–pathogen warfare under changing climate conditions. Curr. Biol. 28:R619–R634. doi:10.1016/j.cub.2018.03.054

Viswanath, K., P. Sinha, S. Naresh Kumar, T. Sharma, S. Saxena, S. Panjwani, … S. M. Shukla. 2017. Simulation of leaf blast infection in tropical rice agro-ecology under climate change scenario. Clim. Change 142:155–167. doi:10.1007/s10584-017-1942-z

Yáñez-López, R., I. Torres-Pacheco, R. G. Guevara-González, M. I. Hernández-Zul, J. A. Quijano-Carranza, and E. Rico-García. 2012. The effect of climate change on plant diseases. Afr. J. Biotechnol. 11:2417–2428.

S Table 1. Lijiangxintuanheigu monogenic lines (LTH MLs) with different genes for blast resistance

Line	Targeted resistance gene	Donor
IRBLa-A[z]	*Pia*	Aichi Asahi
IRBLa-C		CO39
IRBLi-F5	*Pii*	Fujisaka5
IRBLks-F5	*Pik-s*	Fujisaka5
IRBLks-S		Shin2
IRBLk-Ka	*Pik*	Kanto51
IRBLkp-K60	Pik-p	K60
IRBLkh-K3	*Pik-h*	K3
IRBLz-Fu	*Piz*	Fukunishiki
IRBLz5-CA	*Piz5*	C101A51
IRBLzt-T	*Piz-t*	Toride1
IRBLta-K1	*Pita*	K1
IRBLta-CT2		C105TTP2L9
IRBLta-CP1		C101PKT
IRBLb-B	*Pib*	BL1
IRBLt-K59	*Pit*	K59
IRBLsh-S	*Pish*	Shin2
IRBLsh-B		BL1
IRBL1-CL	*Pi1*	C101LAC
IRBL3-CP4	*Pi3(t)*	C104PKT
IRBL5-M	*Pi5(t)*	Moroberekan
IRBL7-M	*Pi7(t)*	Moroberekan
IRBL9-W	*Pi9*	WHD-1S-75-1-127
IRBL12-M	*Pi12*	Moroberekan
IRBL19-A	*Pi19(t)*	Aichi Asahi
IRBLkm-Ts	*Pik-m*	Tsuyuake
IRBL20-IR24	*Pi20(t)*	IR24
IRBLta2-Pi	*Pita-2*	Pi.No.4
IRBLta2-Re		Reiho
IRBL11-Zh	*Pi11*	Zhaiyeqing8
LTH		

[z] Monogenic lines are designated as IRBL (International Rice Research Institute-bred blast-resistant line) followed by the resistance gene then the abbreviation of the resistant donor variety.

S Table 2. Average daily mycelium growth rate and sporulation of four rice blast pathotype clusters of Taiwan cultured at different temperatures

Temperature	Pathotype cluster	Mycelium growth rate (mm day^{-1})		Sporulation (number of conidia $plate^{-1}$)	
12℃	L1	0.269[z]	n[y]	56,700	j
	L2	0.363	m	129,100	ij
	L4	0.374	m	82,600	j
	L5	0.278	n	50,650	j
16℃	L1	0.691	l	96,900	j
	L2	0.705	kl	139,050	ij
	L4	0.763	k	117,650	ij
	L5	0.701	kl	59,400	j
20℃	L1	1.777	g	171,750	ij
	L2	1.692	h	572,050	fg
	L4	1.618	i	388,000	gh
	L5	1.535	j	137,050	ij
24℃	L1	2.561	cde	1,237,200	e
	L2	2.493	e	1,510,100	d
	L4	2.520	de	2,018,900	c
	L5	2.328	f	746,450	f
28℃	L1	2.941	a	651,350	f
	L2	2.809	b	1,506,850	d
	L4	2.971	a	3,306,750	a
	L5	2.984	a	1,173,050	e
32℃	L1	2.529	de	306,500	hi
	L2	2.513	de	1,110,350	e
	L4	2.579	cd	2,620,100	b
	L5	2.633	c	1,047,150	e
36℃	L1	0.005	o	120,650	ij
	L2	0.068	o	195,400	hij
	L4	0.025	o	25,050	j
	L5	0.024	o	149,850	ij
40℃	L1	0	o	0	j
	L2	0	o	0	j
	L4	0	o	0	j
	L5	0	o	0	j

[z] The mean value of each pathotype subgroup represents five isolates.

[y] Values are expressed as the mean of each pathotype subgroup, and means within a column followed by the same letter(s) are not significantly different at the 5% level determined by Fisher's protected least significant difference (PLSD) test.

溫度對臺灣稻熱病菌 (*Pyricularia oryzae*) 四種病原型菌株生長及產孢之影響

陳繹年 [1,*]　吳東鴻 [2]　陳美君 [3]　陳珮臻 [4]

摘要

陳繹年、吳東鴻、陳美君、陳珮臻。2025。溫度對臺灣稻熱病菌 (*Pyricularia oryzae*) 四種病原型菌株生長及產孢之影響。台灣農業研究 74(2):161–175。

氣候變遷引發的溫度與降雨變化，可能影響某些對濕度和溫度敏感的植物有害生物及其媒介生態，進而改變病害的發生率及其時間和空間分布。先前研究顯示，臺灣稻熱病菌 (*Pyricularia oryzae*) 可根據對麗江新團黑谷單基因系 (Lijiangxintuanheigu monogenic lines; LTH MLs) 的致病力，分為 5 個病原型菌系，且這些菌系在棲地溫度上存在差異。本研究針對 4 個主要病原型菌系，每個菌系選取 5 個分離株，分析溫度對其菌絲生長與孢子形成的影響。結果顯示，24–32℃為適合臺灣稻熱病菌生長與繁殖的溫度範圍，其中 28℃為最適溫度。當溫度低於 20℃或高於 36℃時，稻熱病菌的生長和繁殖受到顯著抑制。所有分離株在 36℃下均能存活，但幾乎完全停止生長。整體而言，L4 和 L5 菌系在 32℃下的生長和繁殖優於 24℃；然 L1 和 L2 菌系相對在 24℃下表現更佳。特別是 L4 菌系在 24–32℃間的繁殖能力顯著高於其他 3 個菌系。根據 4 個主要病原型菌系在不同溫度下的菌絲生長與孢子形成能力，推測自 2019 年以來平均氣溫持續上升，可能導致 L4 和 L5 成為臺灣近年流行菌系的主要原因。本研究顯示溫度變化對臺灣稻熱病菌流行的影響，並為應對氣候變遷提供重要的抗病策略參考。

關鍵詞：氣候變遷、菌絲生長速度、稻瘟病菌、產孢、溫度。

投稿日期：2024 年 10 月 17 日；接受日期：2025 年 1 月 23 日。

[*] 通訊作者：sogox@tari.gov.tw
[1] 農業部農業試驗所植物病理組助理研究員。臺灣 臺中市。
[2] 農業部農業試驗所作物組副研究員。臺灣 臺中市。
[3] 農業部農業試驗所植物病理組計畫助理。臺灣 臺中市。
[4] 國立中興大學植物病理學系教授。臺灣 臺中市。

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):177–187 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0007

Research Article

Evaluation of the Use of One-Step Quantitative RT-PCR for Detection of Potato Virus X

Cheng-Ping Kuan[1,*], Ya-Ting Liu[2], Ssu-Yu Lin[3], Mei-Ju Lin[4], Shu Chen[5], and Yin-Hewey Cheng[6]

Abstract

Kuan, C. P., Y. T. Liu, S. Y. Lin, M. J. Lin, S. Chen, and Y. H. Cheng. 2025. Evaluation of the use of quantitative RT-PCR for the detection of potato virus X. J. Taiwan Agric. Res. 74(2):177–187.

This study developed a real-time reverse transcription-polymerase chain reaction (RT-PCR) detection method for potato virus X (PVX) by designing a specific primer pair based on the coat protein (CP) gene. The assay demonstrated a sensitivity approximately 10–100 times higher than conventional RT-PCR for PVX detection. Furthermore, it exhibited high specificity, accurately detecting PVX without cross-reacting with other solanaceous viruses or uninfected healthy plants. The reliability of this method was further confirmed through field testing on PVX-infected potato samples. Due to its high sensitivity and specificity, the real-time RT-PCR assay developed in this study has significant potential for the early detection of PVX infections in potatoes and tomatoes.

Key words: Potato virus X, Real-time RT-PCR, Detection.

INTRODUCTION

Potatoes (*Solanum tuberosum* L.) are susceptible to more than 40 virus species (Martelli *et al.* 2008; Kreuze *et al.* 2020). The principal viruses in potato crops causing significant economic damage in the world are potato virus X (PVX), potato virus Y (PVY), potato virus S (PVS), potato virus A (PVA), potato virus M (PVM), and potato leaf roll virus (PLRV) (Kumar *et al.* 2019). Potatoes are propagated vegetatively using seed tubers, facilitating the rapid and extensive spread of viruses. Therefore, the primary strategy for managing these viral diseases is to use healthy, virus-free seed potatoes and to test mother tubers and tissue culture planting materials to ensure free of virus infection (Kumar *et al.* 2019).

PVX is a member of the Potexvirus genus. Virus particles are filamentous with a single-stranded RNA genome, measuring approximately 515 × 13 nm (Jeevalatha *et al.* 2016). Symptoms caused by PVX infection include mild mottling or necrotic streaks, with highly susceptible potato varieties displaying pale or dark green spots on the leaves and irregular

Received: November 21, 2024; Accepted: February 26, 2025.
* Corresponding author, e-mail: pcr123@tari.gov.tw
1 Associate Research Fellow, Crop Resource and Biotechnology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
2 Project Assistant, Crop Resources and Biotechnology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
3 Assistant Research Fellow, Crop Resource and Biotechnology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
4 Assistant Research Fellow, Plant Pathology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
5 Research Fellow and Division Director, Crop Resources and Biotechnology Division, Taiwan Agricultural Research Institute, Taichung City, Taiwan, ROC.
6 Research Fellow and Division Director, Department of Plant Protection and Utilization, Fengshan Tropical Horticultural Experiment Branch, Taiwan Agricultural Research Institute, Kaoshung, Taiwan, ROC.

small spots between the veins (Bendahmane *et al.* 1997; Tommiska *et al.* 1998). PVX can cause yield reductions ranging from 10% to 30% (Jeevalatha *et al.* 2016), and even 40% to 50% when it is in coinfection with PVA or PVY. PVX spreads primarily through agricultural tools or mechanical contact between healthy and infected plants (Jeevalatha *et al.* 2016; Kumar *et al.* 2019; Rashid *et al.* 2021). The main control measure for PVX is using virus-free seed potatoes (Kumar *et al.* 2019). Developing a straightforward and accurate diagnostic method is thus essential for the early detection of PVX infection.

Various diagnostic methods have been employed to identify PVX in potatoes, including visual inspection, mechanical inoculation onto indicator plants, electron microscopy, and enzyme-linked immunosorbent assay (ELISA) (Kumar *et al.* 2021). However, these techniques are often time-consuming, have low sensitivity, are non-specific, and are unsuitable for use on dormant tubers (Raigond *et al.* 2019). Recent advances have led to the use of more sensitive methods such as reverse transcription-polymerase chain reaction (RT-PCR) (Soliman *et al.* 2000; Yu *et al.* 2008; Jamal *et al.* 2012; Mandal *et al.* 2012), multiplex RT-PCR (Singh *et al.* 2004; Peiman & Xie 2006; Bostan & Peker 2009; Kumar *et al.* 2017). Although some methods can simultaneously detect multiple potato viruses (Agindotan *et al.* 2007; Jeevalatha *et al.* 2016), their sensitivity remains limited. In this study, the improved real-time RT-PCR method using a one-step approach is expected to detect PVX in potato leaves and tuber samples and compared to the RT-PCR method.

MATERIALS AND METHODS

Virus sources

Virus isolates, such as PVX, tobacco mosaic virus (TMV), tomato mosaic virus (ToMV), cucumber mosaic virus (CMV), pepper mild mottle virus (PMMoV), PVY, pepper mosaic virus (PMV), chili vein mosaic virus (CVMV), and pepper vein mottle virus (PVMV), were obtained by Dr. Ting-Ching Deng (former virus specialist in Plant Pathology Division, Taiwan Agricultural Research Institute), and were maintained in tobacco (*Nicotiana benthamiana*) in the greenhouse (Cheng *et al.* 2013). Potatoes suspected of PVX infection were collected in a field in central Taiwan. PVX was inoculated and propagated in tobacco plants (*N. benthamiana*), tomato (*S. lycopersicum*), and potato (*S. tuberosum*).

RNA extraction

The purification method was mainly based on Agindotan (Agindotan *et al.* 2007), with slight modifications. 0.1 gram of tissue, collected from potato leaf/tuber, either PVX-infected or virus-free was ground using liquid nitrogen. The powdered tissue was then extracted with 0.5 mL of extraction buffer (diethyl pyrocarbonate (DEPC)-treated phosphate buffered saline (PBS) buffer (pH 7.4) containing 2% (w/v) polyvinylpyrrolidone-40 (PVP-40), 0.2% (w/v) egg albumin, and 1% (w/v) Na_2SO_3). To 36 µL of crude sap, 4 µL of RNA-secure reagent (20×) (Ambion) was added, mixed thoroughly, and incubated at 60℃ for 10 min. Throughout the experiment, crude sap was diluted using the extraction buffer.

Construction of the PVX-specific gene

The RNA from PVX-infected strains underwent a PCR reaction using the PVX-cp-751-F/R primer (as listed in Table 1). The amplified fragments were cloned into the pGEM-T Easy vector (Promega, Madison, WI, USA) and transformed into *Escherichia coli* (Protech, Taipei, Taiwan). Recombinant vector DNA was purified using the GeneSpin DNA extraction kit (Protech, Taipei, Taiwan). The plasmid containing the full-length PVX cp sequences was amplified by PCR with T7 + PVX-cp-112-F and PVX-cp-751-R primers. The resulting fragment was purified and used as a template for in vitro transcription with T7 RNA polymerase, following the MEGAscript® Kit protocol (Ambion™, Austin, TX, USA). The reaction products were dissolved in nuclease-free water, and the RNA concentration was calculated and serially diluted for sensitivity testing.

Table 1. The primers and probes used in this experiment.

Primers and probe	Sequence (5′–3′)[z]	Amplicon size (bp)
PVX-cp-751-F	TACTCGAAAGATGTCAGCACCAGCT	751
PVX-cp-751-R	GGGGTAGGCGTCGGTTATGTAGA	
PVX-cp-112-F	CCTATTCCAACGGCATCAG	112
PVX-cp-112-R	GTCAGCATCCAGTTCCATAC	
PVX-cp-112-Probe	TCGCTGCTGCCAGTCTGGC	
T7 + PVX-cp-112-F	FAM[y]-TAATACGACTCACTATAGGCCTATTC CAACGGCATCAG-BHQ1[y]	

[z] GeneBand Accession no. AF272736
[y] FAM: 6-carboxyfluorescein; BHQ1: black hole x quencher1

Design of PVX primers and probes

Primers and probes were designed using Primer Express™ software (Applied Biosystems, Foster City, CA, USA). The primers (PVX-cp-112-F/R) were specifically targeted to the cp gene sequence of PVX, with an expected product size of 112 bp. The RT-PCR amplified sequence included a binding site for the specific fluorescent probe PVX-probe (Table 1) to ensure that during nucleic acid amplification, the specific fluorescent probe generates fluorescence upon polymerase degradation, allowing the real-time RT-PCR machine to detect the fluorescent signal. The 5′ and 3′ ends were labeled with the fluorescent dyes FAM (6-carboxyfluorescein, excitation wavelength = 494 nm) and minor groove binder (MGB) (excitation wavelength = 520 nm), respectively.

RT-PCR and real-time RT-PCR methods

The RT-PCR reaction conditions were set to 50℃ for 15 min, and 95℃ for 3 min, followed by 40 cycles of 95℃ for 15 s, 60℃ for 30 s, and 72℃ for 30 s, with a final extension at 72℃ for 5 min and holding at 16℃. The PCR reagents included SuperScript™ III RT/Platinum™ Taq Mix (Invitrogen, San Diego, CA, USA) 0.5 μL, 2× Reaction Mix 12.5 μL, each 0.2 μM of PVX-cp-112 F/R primer 1 μL, probe 50 nM, Rox 50 nM, and plant RNA in a total reaction volume of 25 μL. The real-time RT-PCR conditions were 50℃ for 5 min, and 95℃ for 2 min, followed by 40 cycles of 95℃ for 3 s and 60℃ for 30 s. The real-time RT-PCR machine used was the ABI PRISM® 7500 Sequence Detection System (Applied Biosystems, Foster City, CA, USA).

ELISA

This experiment followed the method outlined by Clark & Adams (1977). A 0.2 g sample of diseased leaf tissue (tomato or potato) was ground in 2 mL of 15 mM sodium carbonate buffer (pH 9.6) and added to an ELISA plate (100 μL $well^{-1}$). Each sample was tested in duplicate, and the plates were incubated at 37℃ for 4 h. The plates were washed three times with 1× PBST (137 mM NaCl, 1.5 mM KH_2PO_4, 1 mM Na_2HPO_4, 0.05% Tween 20, pH 7.4), followed by the addition of PVX antibodies (DSMZ; Mikroorganismen und Zellkulturen GmbH, Braunschweig, Germany) and a 2-hour incubation at 37℃. After washing three times with 1× PBST, goat anti-rabbit immunoglobulin secondary antibodies (Invitrogen, San Diego, CA, USA, 100 μL $well^{-1}$), dissolved in phosphate buffer (137 mM NaCl, 1.5 mM KH_2PO_4, 1 mM Na_2HPO_4, 0.05% Tween 20, pH 7.4), were added. The plates were incubated at 37℃ for 2 h. After washing four times with 1× PBST, a 150 μL $well^{-1}$ solution of 1 mg mL^{-1} alkaline phosphatase enzyme substrate (ρ-NPP, Amresco, Solon Ind., OH, USA) was added for color development. After 20 to 30 min of reaction, the absorbance at 405 nm was measured using an ELISA reader (PTI max microplate reader, Molecular Devices, Sunnyvale, CA, USA).

RESULTS

Specificity of RT-PCR and real-time RT-PCR for PVX detection

To develop primers and probes specific to PVX, this study utilized sequence alignment of the highly conserved region of the PVX coat protein (cp) gene. The designed primers, PVX-cp-112-F and PVX-cp-112-R, along with the probe PVX-cp-112-probe (listed in Table 1), were tested for specificity against a variety of other Solanaceae viruses, including PMMoV, PVX, TMV, ToMV, PVMV, CVMV, and PMV from tomato or pepper and PVY from potato. PMMoV, TMV, ToMV, PVY, PVMV, CVMV, and PMV were used by RT-PCR and real-time RT-PCR assays, respectively. The healthy plants of tomato were as healthy controls. A no-template control (NTC) using ddH_2O was also included to ensure no contamination. The agarose gel electrophoresis analysis revealed that the PVX-positive controls, which included cloned PVX plasmids and PVX-infected plants, produced a specific 112 bp nucleic acid fragment. No amplification was detected in the samples from other Solanaceae viruses or the healthy plants (Fig. 1). This result confirms the high specificity of the primers and probe for PVX.

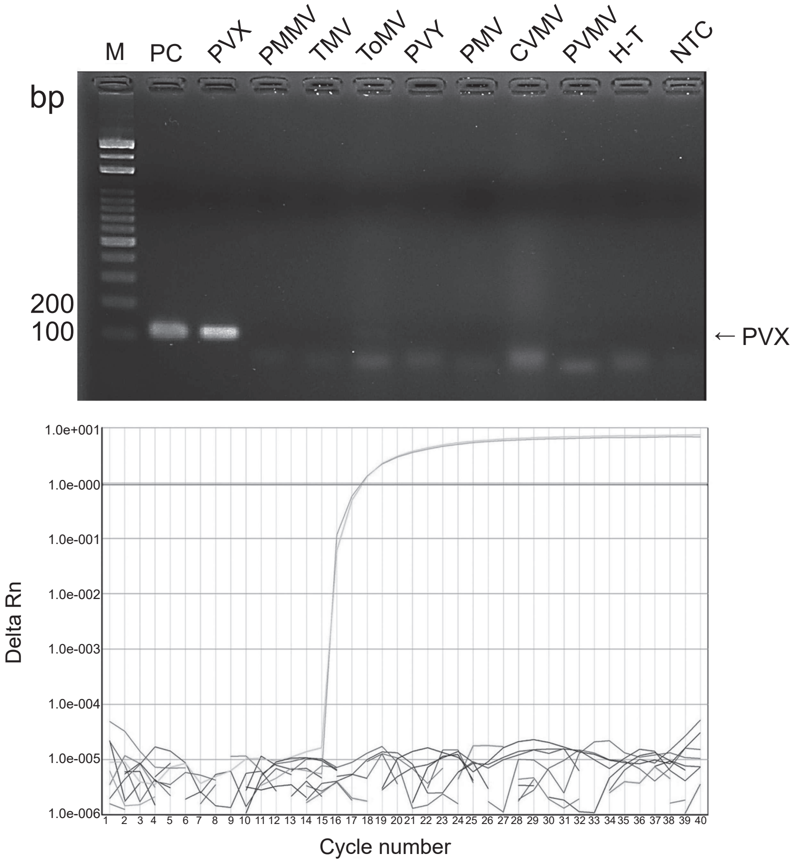

Fig. 1. Specificity evaluation of potato virus X (PVX) detection based on the reverse transcription-polymerase chain reaction (RT-PCR) (upper) and real-time RT-PCR (lower) assays. Amplification of PVX, pepper mild mottle virus (PMMV), tobacco mosaic virus (TMV), tomato mosaic virus (ToMV), potato virus Y (PVY), pepper mosaic virus (PMV), chili vein mosaic virus (CVMV), and pepper vein mottle virus (PVMV)-infected plants by RNA extracts. Health tomato samples as negative control (H-T). In RT-PCR, a 112-bp amplicon was generate only from positive control (PC) and PVX. Lane NTC: No Template Control and Lane M: 100 bp ladder.

Additionally, real-time RT-PCR results were consistent with those of RT-PCR, showing positive signals only for the PVX-positive controls, with Ct values of 12.89 and 15.1 for the PVX plasmid and PVX-infected plants, respectively. No reactions were observed for other viruses, healthy plants, or the negative controls. These findings indicate that the primers and probes are highly specific for PVX detection, without cross-reactivity with other Solanaceae viruses.

Sensitivity test of PVX

To understand the relationship between the detected viral load and the detection limit of PVX in tomatoes and potatoes after artificial infection, RT-PCR and ELISA were used for Evaluation. The detection limit of ELISA in tomatoes reached 10^6 dilution factor, while in potatoes, it reached 10^3. The results indicate that the detection limit in tomatoes is approximately 1,000 times greater than in potatoes. The detection limit of RT-PCR in tomatoes reached 10^8 dilution factor, while in potatoes, it reached 10^5. The results indicate that the detection limit in tomatoes is approximately 1,000 times greater than in potatoes (Table 2). For the same material (tomato/potato), the sensitivity of RT-PCR is approximately 100 times higher than that of ELISA.

The sensitivities of the RT-PCR and real-time RT-PCR methods for detecting PVX were evaluated using whole RNA extracted from PVX-infected plants and in vitro transcribed PVX coat protein RNA. The PVX coat protein (CP) RNA was detected at a concentration of 10^3 copies using RT-PCR and 10 copies using real-time RT-PCR (Fig. 2 and Fig. 3). These results indicate that the real-time RT-PCR method is approximately 100 times more sensitive than traditional RT-PCR in detecting low levels of PVX.

Detection of PVX in potato from field samples

The detection of PVX in potato samples was conducted by extracting total RNAs from the leaf/tuber tissue of suspected infected plants. Healthy potato leaves and a NTC were negative controls. The presence of PVX was assessed using RT-PCR, real-time RT-PCR, and ELISA. According to the results, both RT-PCR and real-time RT-PCR could successfully detect PVX from field samples (Table 3). Seven out of 20 field samples

Table 2. Comparison of reverse transcription-polymerase chain reaction (RT-PCR) and enzyme-linked immunosorbent assay (ELISA) for detecting potato virus X (PVX) using the detection limit of extracted infected leaf samples.

	Tomato[z]		Potato[z]	
Dilution factor	RT-PCR	ELISA $A_{405\ nm}$	RT-PCR	ELISA $A_{405\ nm}$
1	+	3.484+	+	3.064+
1 × 10	+	3.545+	+	2.116+
1×10^2	+	3.490+	+	1.134+
1×10^3	+	2.482+	+	0.266+
1×10^4	+	0.702+	+	0.087–
1×10^5	+	0.483+	+	0.076–
1×10^6	+	0.295+	–	0.070–
1×10^7	+	0.161–	–	0.090–
1×10^8	+	0.102–	–	0.085–
1×10^9	–	0.070–	–	0.084–
1×10^{10}	–	0.105–	–	0.101–
H-CK	–	0.105–	–	0.101–

[z] Plant tissue testing starting quantity: 0.1 g (RT-PCR); 0.2 g (ELISA).

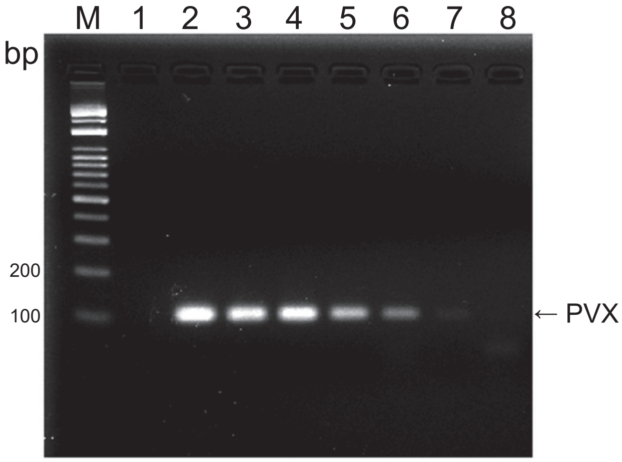

Fig. 2. The detection limit of reverse transcription-polymerase chain reaction (RT-PCR) assay based on cRNA copy number of potato virus X (PVX). PVX copy number: 1: NTC 2. Positive control, 3: 10^7; 4: 10^6; 5: 10^5; 6: 10^4; 7: 10^3; 8: 10^2 copies uL^{-1}.

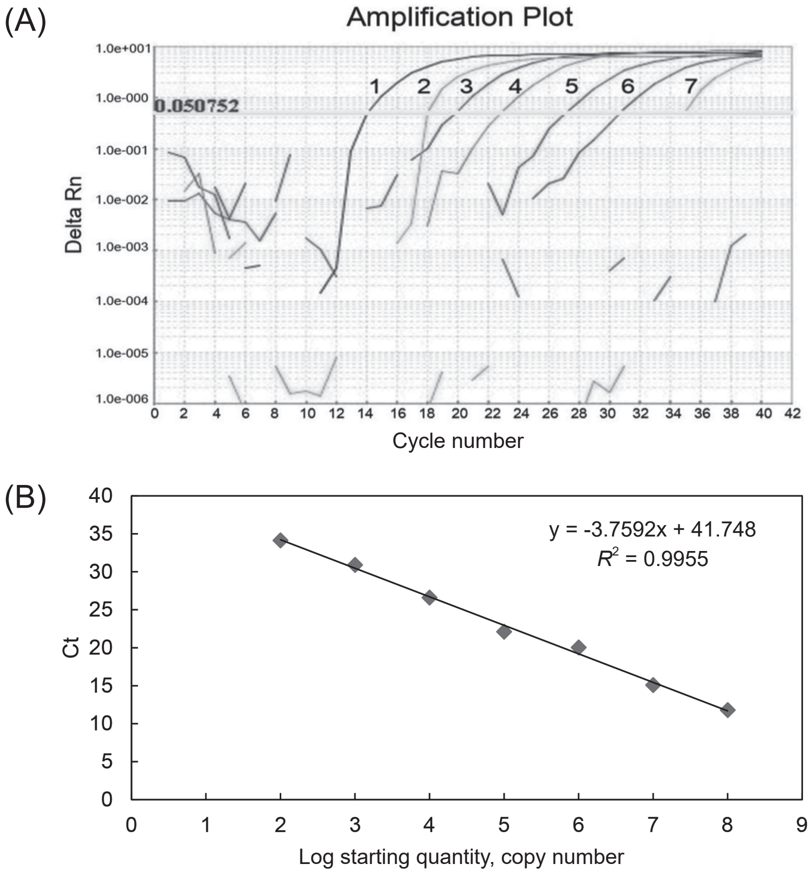

Fig. 3. Sensitivity detection of potato virus X (PVX) using real-time reverse transcription-polymerase chain reaction (RT-PCR) assay: (A) The results of real-time RT-PCR; and (B) The real-time RT-PCR was plotted as a standard curve. PVX copy number: 1: 10^7; 2: 10^6; 3: 10^5; 4: 10^4; 5: 10^3; 6: 10^2; 7: 10^1 copies uL^{-1}.

Table 3. Comparison of different methods for detecting potato virus X (PVX) infection in field-grown potatoes.

Tissues[z]	RT-PCR	Real-time RT-PCR		Enzyme-linked immuno-sorbent assay (ELISA)	$A_{405\ nm}$
			Ct		
S1	+[y]	+	30.41	+	0.452
S2	+	+	29.82	+	0.771
S3	–[y]	–	ND	–	0.109
S4	–	–	ND	–	0.142
S5	–	–	ND	–	0.195
S6	+	+	24.16	+	0.539
S7	–	–	ND	–	0.072
S8	–	–	ND	–	0.020
S9	–	–	ND	–	0.084
S10	+	+	29.92	+	0.761
S11	–	–	ND	–	0.122
S12	–	–	ND	–	0.141
S13	–	–	ND	–	0.084
S14	+	+	31.17	–	0.057
S15	+	+	21.87	+	0.947
S16	–	–	ND	–	0.139
S17	–	–	ND	–	0.172
S18	+	+	30.09	–	0.160
S19	–	–	ND	–	0.184
S20	–	–	ND	–	0.161
Positive control[x]	+	+	12.51	+	2.939
Negative control[x]	–	–	–	–	0.212
NTC[x]	–	–	–	–	0.162

[z] S1–S15: leave tissues; S16–S20: tuber tissues.
[y] "+" indicates positive reaction, whereas "–" indicates a negative reaction.
[x] Negative control: healthy tomato; Positive control: PVX-infected tomato; NTC: no template control.

(leaves or tubers) were positive for PVX using RT-PCR. In contrast, only five samples were positively tested using ELISA.

DISCUSSION

PVX is a highly destructive virus that causes a significant threat to potato crops due to its ease of transmission through mechanical contact. It has also been found in potato fields in Taiwan (Deng *et al.* 1992). Effective management of PVX requires early detection or using of virus-resistant cultivars. PVX is primarily transmitted through potato tubers, the application of this real-time RT-PCR assay for large-scale testing of potato tubers will add substantial value to the research. Currently, RT-PCR and ELISA are widely used as PVX detection methods. Internationally, multiplex detection methods for potato viruses have been developed, allowing the detection of multiple viruses (PVX, PVY, PVA, and PLRV). However, real-time RT-PCR thermocycler have limitations (limited by the number of instrument fluorescence channels). As a result, it is not possible to simultaneously detect all four viruses while incorporating an additional internal control for validation (Agindotain *et al.* 2007). The real-time RT-PCR method developed in this study amplifies a 112 bp fragment of the PVX viral gene. One key advantage of this method is its ability to prepare

samples in a single reaction tube, which eliminates the need for a separate cDNA synthesis step and enables one-step nucleic acid amplification. This simplifies the detection process by reducing the number of operational steps and enhances the efficiency of virus detection.

Detection from diluted PVX-infected leaf tissue showed that, regardless of whether RT-PCR or ELISA was used, the detectable dilution factor in infected tomato tissue could detect lower than that in potato tissue. This suggests that the PVX concentration in tomatoes is higher than in potatoes. This phenomenon requires more sampling and repeated experiments for validation, as the current results are only from a preliminary test. There is no related research mentioned, but PVX can infect both tomato and potato plants, causing varying symptoms. In tomatoes, PVX infection leads to mosaic patterns and slight stunting, while in potatoes, it typically results in mild mosaic symptoms or remains latent. The severity of PVX symptoms can be influenced by factors such as mixed infections with PVY (Verchot 2021). Sensitivity tests indicated that the real-time RT-PCR method developed in this study is comparable to previous findings by Agindotan *et al.* (2007), demonstrating at least a 10-fold increase in sensitivity. Notably, while Agindotan *et al.* (2007) utilized a two-step real-time RT-PCR method, this study's one-step approach streamlines the process, further improving detection efficiency. In other words, the sensitivity results showed that the real-time RT-PCR in this study is 100 times more sensitive than conventional RT-PCR and 10 times superior to the two-step method. Field tests on 20 potato samples (leaves or tubers) revealed that the real-time RT-PCR method was consistent with traditional RT-PCR in terms of positive virus detection. However, the real-time RT-PCR assay detected more positive samples than double-antibody sandwich ELISA (DAS-ELISA), RT-PCR identified 7 positive samples, whereas ELISA detected only 5 samples. In addition, the use of potato tubers showed that only one sample was detected positively by RT-PCR and real-time RT-PCR; however, ELISA could not detect the target virus. The inability of DAS-ELISA to detect PVX in some potato tuber samples might be due to the viral concentration being below the detection threshold or the uneven distribution of the virus in dormant tubers like PVY in potato (Whitworth *et al.* 2012). PVX tends to multiply during the sprouting process (Betti *et al.* 2012), leading to a higher viral load in sprouts, which makes it easier to be detected. Consequently, sprouting tuber samples are more suitable for DAS-ELISA detection. The one-step real-time RT-PCR assay demonstrated a 10-fold higher sensitivity compared to RT-PCR, confirming its superiority in detecting PVX, particularly in cases of low viral load. Moreover, the consistency between RT-PCR and real-time RT-PCR in detecting positive samples reinforces the reliability of the developed assay. Some samples that tested negative by ELISA were detected as positive by RT-PCR, highlighting the limitations of ELISA in detecting low-concentration or unevenly distributed viruses.

Previous studies have demonstrated that real-time RT-PCR is more sensitive than conventional RT-PCR for detecting plant RNA viruses (Babu *et al.* 2017; Kapoor *et al.* 2017; DeShields *et al.* 2019; Mohandas & Bhat 2020; Naveen & Bhat 2020; Wang *et al.* 2020). In addition, since RNA extraction in this study does not require the use of commercial kits and only utilizes simple isolation without complex procedures, it can reduce detection costs for large-scale sample screening. With minimal sample preparation requirements, the one-step real-time RT-PCR assay exhibits high resistance to inhibitors found in plant tissues, thereby improving specificity and sensitivity. The developed one-step real-time RT-PCR assay represents a significant advancement in PVX detection technology. Its rapid, sensitive, and specific detection capabilities, make it an ideal alternative to conventional RT-PCR for use in

tissue culture plants, virus-free certification programs, and screening of PVX-resistant cultivars. By facilitating early detection and reducing the spread of PVX, this assay contributes to more effective management of potato crops, ultimately supporting agricultural productivity and sustainability.

REFERENCES

Agindotan, B. O., P. J. Shiel, and P. H. Berger. 2007. Simultaneous detection of potato viruses, PLRV, PVA, PVX and PVY from dormant potato tubers by TaqMan® real-time RT-PCR. J. Virol. Methods 142:1–9. doi:10.1016/j.jviromet.2006.12.012

Babu, B., B. K. Washburn, T. S. Ertek, S. H. Miller, C. B. Riddle, G. W. Knox, … M. L. Paret. 2017. A field-based detection method for Rose rosette virus using isothermal probe-based Reverse transcription-recombinase polymerase amplification assay. J. Virol. Methods 247:81–90. doi:10.1016/j.jviromet.2017.05.019

Bendahmane, A., K. Kanyuka, and D. C. Baulcombe. 1997. High-resolution genetical and physical mapping of the Rx gene for extreme resistance to potato virus X in tetraploid potato. Theor. Appl. Genet. 95:153–162. doi:10.1007/s001220050543

Betti, C., C. Lico, D. Maffi, S. D'Ageli, M. M. Altamura, E. Benvenuto, ... S. Baschieri. 2012. Potato virus X movement in *Nicotiana benthamiana*: New detailsrevealed by chimeric coat protein variants. Mol. Plant Pathol. 13:198–203. doi:10.1111/J.1364-3703.2011.00739.X

Bostan, H. and P. Peker. 2009. The feasibility of tetraplex RT-PCR in the determination of PVS, PLRV, PVX and PVY from dormant potato tubers. Afr. J. Biotechnol. 8:4043–4047.

Cheng, Y. H., T. C. Deng, C. C. Chen, C. P. Kuan, and C. A. Chang. 2013. Identification and occurrence of Pepper mottle virus isolated from Peppers in Taiwan. J. Taiwan Agric. Res. 62:360–371. (in Chinese with English abstract) doi:10.6156/JTAR/2013.06204.06

Clark, M. F. and A. N. Adams. 1977. Characteristics of the microplate method of enzyme-linked immunosorbent assay for the detection of plant viruses. J. Gen. Virol. 34:475–483. doi:10.1099/0022-1317-34-3-475

Deng, T. C., S. J. Tsao, S. W. Tsai, C. H. Huang, and M. M. Tseng. 1992. Occurrence of potato viruses in Taiwan and resistance to virus Y of some promising clones as determined by ELISA. J. Agric. Res. China 41:361–370. (in Chinese with English abstract) doi:10.29951/JARC.199212.0007

DeShields, J. B., N. Moroz, L. E. Braley, G. A. Mora-Romero, and K. Tanaka. 2019. Recombinase polymerase amplification (RPA) for the rapid isothermal detection of *Spongospora subterranean* f. sp. *subterranea* and potato mop-top Virus. Am. J. Potato Res. 96:617–624. doi:10.1007/s12230-019-09750-7

Jamal, A., L. Korsten, and R. A. A. Van der Vlugt. 2012. Real-time quantitative RT-PCR for the detection of potato virus X in potato plants. J. Virol. Methods 185:1–7. doi:10.1007/BF02360415

Jeevalatha, A., P. Kaundal, R. Kumar, B. Raigond, M. Gupta, A. Kumar, ... B. P. Singh. 2016. Analysis of the coat protein gene of Indian *Potato virus X* isolates for identification of strain groups and determination of the complete genome sequence of two isolates. Eur. J. Plant Pathol. 145:447–458. doi:10.1007/s10658-016-0858-1

Kapoor, R., N. Srivastava, S. Kumar, R. K. Saritha, S. K. Sharma, R. K. Jain, and V. K. Baranwal. 2017. Development of a recombinase polymerase amplification assay for the diagnosis of banana bunchy top virus in different banana cultivars. Arch. Virol. 162:2791–2796. doi:10.1007/s00705-017-3399-9

Kreuze, J. F., J. A. C. Souza-Dias, A. Jeevalatha, A. R. Figueira, J. P. T. Valkonen, and R. A. C. Jones. 2020. Viral diseases in potato. p.389–430. *in*: The potato crop: Its agricultural, nutritional and social contribution to humankind. (Campos, H. and O. Ortiz. eds.) Springer. Cham, Switzerland. 518 pp. doi:10.1007/978-3-030-28683-5_11

Kumar, R., A. Jeevalatha, R. Baswaraj, S. Sharma, and M. Nagesh. 2017. A multiplex RT-PCR assay for simultaneous detection of five viruses in potato. J. Plant Pathol. 99:37–45.

Kumar, R., P. Kaundal, R. K. Tiwari, S. Siddappa, H. Kumari, K. C. Naga, and M. Kumar. 2021. Rapid and sensitive detection of potato virus X by one-step reverse transcription-recombinase polymerase amplification method in potato leaves and dormant tubers. Mol. Cell. Probes 58:101743. doi:10.1016/j.mcp.2021.101743

Kumar, R., R. K. Tiwari, A. Jeevalatha, P. Kaundal, S. Sharma, and S. K Chakrabarti. 2019. Potato viruses and their diagnostic techniques: An overview. J. Pharm. Phytochem. 8:1932–1944.

Mandal, B., A. Kumar, P. Rani, and R. K. Jain. 2012. Complete genome sequence, phylogenetic relationships and molecular diagnosis of an Indian isolate of potato virus X. J. Phytopathol. 160:1–5. doi:10.1111/

j.1439-0434.2011.01848.x

Martelli, G. P., M. J. Adams, J. F. Kreuze, and V. V. Dolja. 2008. Family Flexiviridae: A case study in virion and genome plasticity. Annu. Rev. Phytopathol. 45:73–100. doi:10.1146/annurev.phyto.45.062806.094401

Mohandas, A. and A. I. Bhat. 2020. Recombinase polymerase amplification assay for the detection of piper yellow mottle virus infecting black pepper. Virus Dis. 31:38–44. doi:10.1007/s13337-019-00566-x

Naveen, K. P. and A. I. Bhat. 2020. Reverse transcriptase loop-mediated isothermal amplification and reverse transcriptase recombinase amplification assays for rapid and sensitive detection of cardamom vein clearing virus. 3 Biotech. 10:250. doi:10.1007/s13205-020-02238-w

Peiman, M. and C. Xie. 2006. Development and evaluation of a multiplex RT-PCR for detecting main viruses and a viroid of potato. Acta Virol. 50:129–133. doi:10.4149/av_2017_403

Raigond, B., A. Verma, S. Roach, T. Kochhar, Shilpa, J. Arjunan, ... S. K. Chakrabarti. 2019. One-step reverse transcription loop-mediated isothermal amplification: A simple, sensitive and rapid assay for detection of potato virus X in potato leaves and tubers. Indian Phytopathol. 72:321–328. doi:10.1007/s42360-019-00147-4

Rashid, M. O., J. H. Li, Q. Liu, Y. Wang, and C. G. Han. 2021. Molecular detection and identification of eight potato viruses in Gansu province of China. Curr. Plant Biol. 25:100184. doi:10.1016/j.cpb.2020.100184

Singh, R. P., A. D. Dilworth, M. Singh, and D. L. McLaren. 2004. Evaluation of a simple membrane-based nucleic acid preparation protocol for RT-PCR detection of potato viruses from aphid and plant tissues. J. Virol. Methods 121:163–170. doi:10.1016/j.jviromet.2004.06.012

Soliman, A. M., A. A. Shalaby, B. N. Barsoum, G. G. Mohamed, M. K. Nakhla, H. M. Mazyad, and D. P. Maxwell. 2000. Molecular characterization and RT-PCR-ELISA detection of a potato virus X (PVX) isolate from Egypt. Ann. Agric. Sci. (Cairo) 4:1791–1804.

Tommiska, T. J., J. H. Hämäläinen, K. N. Watanabe, and J. P. T. Valkonen. 1998. Mapping of the gene Nxphu that controls hypersensitive resistance to potato virus X in *Solanum phureja* IvP35. Theor. Appl. Genet. 96:840–843. doi:10.1007/s001220050810

Verchot, J. 2021. Potato virus X: A global potato-infecting virus and type member of the Potexvirus genus. Mol. Plant Pathol. 23:315–320.

Wang, Y., R. Chen, X. Nie, Z. Zhong, C. Li, K. Li, and B. Nie. 2020. Rapid and sensitive detection of potato virus Y by isothermal reverse transcription-recombinase polymerase amplification assay in potato. Mol. Cell. Probes 50:101505. doi:10.1016/j.mcp.2019.101505

Whitworth, J. L., P. B. Hamm, and P. Nolte. 2012. Distribution of potato virus Y strains in tubers during the post-harvest period. Am. J. Pot. Res. 89:136–141. doi:10.1007/s12230-012-9235-6

Yu, X. Q., H. Y. Wang, Y. F. Lan, X. P. Zhu, X. D. Li, Z. F. Fan, ... Y. Y. Wang. 2008. Complete genome sequence of a Chinese isolate of Potato virus X and analysis of genetic diversity. J. phytopathology 156:346–351. doi:10.1111/j.1439-0434.2007.01365.x

使用單步驟定量 RT-PCR 法於馬鈴薯 X 病毒檢測之評估

關政平[1,*] 劉雅婷[2] 林思妤[3] 林玫珠[4] 陳述[5] 鄭櫻慧[6]

摘要

關政平、劉雅婷、林思妤、林玫珠、陳述、鄭櫻慧。2025。使用單步驟定量 RT-PCR 法於馬鈴薯 X 病毒檢測之評估。台灣農業研究 74(2):177–187。

本研究依據馬鈴薯 X 病毒 (potato virus X; PVX) 之鞘蛋白 (coat protein) 基因設計專一性引子對，利用即時反轉錄聚合酶連鎖反應 (real-time reverse transcription-polymerase chain reaction; real-time RT-PCR) 與 TaqMan 螢光探針，建立馬鈴薯 X 病毒的檢測技術。本研究所開發之 real-time RT-PCR 法的靈敏度，在檢測 PVX 上相較於 RT-PCR 法，提高約 10–100 倍，此外，此檢測具有高度特異性，可成功檢測 PVX，且不會與其他茄科病毒或未感染的健康植物發生交叉反應。透過檢測田間感染 PVX 的馬鈴薯，進一步確認此檢測方法的穩定性。有鑑於 real-time RT-PCR 的高特異性和敏感性，本研究所開發的 real-time RT-PCR 檢測在評估馬鈴薯或番茄受 PVX 感染的早期檢測具有高度應用效益。

關鍵詞：馬鈴薯 X 病毒、即時定量 RT-PCR、偵測。

投稿日期：2024 年 11 月 21 日；接受日期：2025 年 2 月 26 日。

[*] 通訊作者：pcr123@tari.gov.tw
[1] 農業部農業試驗所遺傳資源及生物技術組副研究員。臺灣 臺中市。
[2] 農業部農業試驗所遺傳資源及生物技術組計畫助理。臺灣 臺中市。
[3] 農業部農業試驗所遺傳資源及生物技術組助理研究員。臺灣 臺中市。
[4] 農業部農業試驗所植物病理組助理研究員。臺灣 臺中市。
[5] 農業部農業試驗所遺傳資源及生物技術組研究員兼組長。臺灣 臺中市。
[6] 農業部農業試驗所鳳山熱帶園藝試驗分所植物保護及園產品加工系研究員兼系主任。臺灣 高雄市。

台灣農業研究 (J. Taiwan Agric. Res.) 74(2):189–204 (2025)
https://doi.org/10.6156/JTAR.202506_74(2).0008

研究報告

臺灣水稻害蟲名錄之修訂

黃守宏 [1]　賴柏羽 [2,*]　王泰權 [3,*]

摘要

黃守宏、賴柏羽、王泰權。2025。臺灣水稻害蟲名錄之修訂。台灣農業研究 74(2):189–204。

水稻為臺灣主要糧食作物，稻米的安全生產攸關人民生活富足與國家安定。水稻害蟲名錄之建立可提供害蟲生態與管理的重要參考資訊。根據往昔紀錄，臺灣水稻害蟲 (蟎) 曾紀錄有 59–111 種，經重新修訂結果顯示，目前計有害蟲種類 107 種與蟎類 1 種，並排除方異距蝗 (*Heteropternis respondens* (Walker, 1859)) 等 34 種疑問種。

關鍵詞：臺灣、水稻、害蟲與害蟎名錄。

前言

水稻 (*Oryza sativa* Linn.)、小麥及玉米為全世界人口之三大主要糧食作物，供應全人類 50% 以上之熱量來源。在亞洲地區，全球 90% 的水稻種植與消費量在此區域。臺灣地處熱帶與亞熱帶，高溫多雨的氣候適合水稻種植，臺灣在明朝末年開始引進水稻，以種植陸稻 (upland rice) 為主，期間有關水稻害蟲紀錄出現於《臺灣府誌》等『地方誌』中，但名稱為蛾、蟬等，並未說明其對水稻之危害方式與發生情況，甚難辨明是否為真正的水稻害蟲 (Cheng & Chu 1999)。在日治初期 (1895 年)，日本於臺灣成立水稻專責研究機構，水稻 (灌溉稻，irrigated rice) 種植面積與產量迅速增加，逐漸有系統地進行水稻蟲害研究與紀錄 (Miwa 1943)；臺灣光復 (1945 年) 後，政府也積極投入大量人力與經費進行研究，隨著灌溉系統的改善、化學肥料及藥劑大量使用等措施，此時期之水稻進入大量增產期，於 1975 年種植面積達到最高 (79 萬餘公頃)，糙米產量約 3,156 kg ha^{-1} (Huang 1999)，但水稻害蟲發生蟲相隨之改變，早期紀錄之 5 大害蟲 (稻黑椿象 (*Scotinophara lurida* (Burmeister))、稻負泥蟲 (*Oulema oryzae* (Kuwayama)) 及稻鐵甲蟲 (*Dicladispa armigera* (Olivier)) 等) 逐漸式微，而個體小、世代短之飛蝨類與葉蟬類害蟲則逐漸崛起 (Cheng & Huang 2009)；後因臺灣糧食生產過剩，國人飲食習慣改變等，稻田生產政策改為轉作調整等方向，蟲害管理方式進入以生態為基礎之綜合管理方式，蟲害發生隨之更迭，截至 2023 年為止，栽培面積已降至 22.2 萬公頃，糙米產量約 5,161 kg ha^{-1} (https://agrstat.moa.gov.tw/sdweb/public/inquiry/InquireAdvance.aspx)；期間，除長距離遷移性害蟲於遷出地區之發生種類及族群消長變化，如褐飛蝨 (*Nilaparvata lugens* (Stål))、白背飛蝨 (*Sogatella furcifera* (Horváth)) 及水稻縱捲葉蟲 (*Cnaphalocrocis medinalis* (Guenée)) 等，進而影響遷入地區 (臺灣) 蟲害發生變化外，隨著國際貿易頻繁，外來種 (如水稻水象鼻蟲 (*Lissorhoptrus oryzophilus* Kuschel)) 隨著貨物的入侵而立足於臺灣，嚴重之危害性除對產量造成重大影響，也改變原有臺灣蟲害管理模式，為臺灣糧食安全生產需面臨調整之重大問題 (Huang *et al.* 2010)。

近年來全球氣候變遷情況日趨嚴重，其中以溫度上升現象最為明顯，臺灣逐漸變成熱帶

投稿日期：2024 年 12 月 3 日；接受日期：2025 年 2 月 11 日。
[*] 通訊作者：tukust94413@tari.gov.tw; insect6925@mail.kdais.gov.tw
[1] 農業部農業試驗所嘉義分所植物保護系副研究員兼系主任。臺灣 嘉義市。
[2] 農業部農業試驗所嘉義分所植物保護系助理研究員。臺灣 嘉義市。
[3] 農業部高雄區農業改良場作物環境科助理研究員。臺灣 屏東縣。

型氣候環境，原本存在臺灣的熱帶型水稻害蟲發生逐漸遽增，南洋地區的熱帶地區種類也很有可能向北擴散而入侵至臺灣，馬來亞黑椿象 (Malayan rice black bug, *Scotinophara coarctata* (Fabricius))，亦為政府需要注意之課題 (Lai *et al.* 2023)。害蟲名錄之建立除提供害蟲發生紀錄外，更可搭配環境改變及蟲害發生更迭資料，提供分析之參考，作為政府對於臺灣未來糧食安全管理策略擬定之重大參考資訊。

材料與方法

名錄依據與分類文獻來源蒐集

本名錄修訂方法包含蒐集日治時期與臺灣光復至今發表有關臺灣水稻害蟲之調查與名錄等報告為基礎，其中摒除以往文獻中未附參考文獻之存疑有害生物紀錄，達到本研究增修訂有害生物名錄的正確性。修正名錄內容包含每一害蟲 (蟎) 所屬之分類階層 (taxonomic category)、學名 (scientific name)、中英文俗名 (common name)、引用文獻 (cited reference)、危害部位及害蟲階級 (category of pest) 等資訊。害蟲分類階級採用拉丁文與中文並列，引用之文獻亦詳列出作者、發表年代及引用資料出處，以方便讀者查詢。同物異名因繁多不予羅列，亦參考全球生物多樣性資訊機構 (Global Biodiversity Information Facility; GBIF) 的 GBIF Backbone Taxonomy (https://www.gbif.org/dataset/d7dddbf4-2cf0-4f39-9b2a-bb099caae36c)、EPPO Global Database (https://gd.eppo.int/)、ScaleNet (https://www.sel.barc.usda.gov/scalenet/query.htm) 及 CABI Digital Library (https://www.cabidigitallibrary.org/action/doSearch?ConceptID=50006) 進行查詢。害蟲危害之分級標準依 Pena *et al.* (1997) 報告指出，如在未採取任何防治措施情況下，害蟲族群經繁殖與危害，對作物生長與產量造成嚴重影響者，為主要害蟲 (major or key pest)；害蟲對作物造成經濟損失不高，但也有可能取代成為主要害蟲種類者，為次要害蟲 (secondary or minor pest)；於特定時間發生之區域性害蟲種類者，為偶發性害蟲 (occasional pest)；先前未被記錄為害蟲，經調查與飼育後，確定可以為害水稻與完成生活史者，則以新興害蟲 (emerging pest) 表示。

水稻田間害蟲調查

本調查由筆者自 2015–2023 年，於嘉義縣民雄鄉有機栽培水稻田區 (0.3 ha) 中，每 2 wk 以目視與掃網調查水稻上之有害生物種類，每次目視 120 叢水稻與來回網掃 (網徑 37 cm，網深 75 cm，蟲桿長 100 cm) 20 次；期間亦至各縣市田區中採樣，所採集到可疑與無法鑑定之有害生物種類者，標本送請農業部農業試驗所應用動物組昆蟲分類研究室協助鑑定。針對文獻上未記錄之害蟲種類，則攜回實驗室或以套網飼育，若該害蟲可取食危害並完成生活史，則確定其為害蟲種類，只有某一時期危害者僅能判定水稻為其食料作物 (food plant)，並非其寄主植物 (host plant) (Shih *et al.* 2013)。

臺灣水稻害蟲 (蟎) 存疑種之判定

為進行臺灣水稻害蟲 (蟎) 之判定，評定標準以 Shih *et al.* (2013) 報告為主，其發生若為 (1) 首次被記錄為臺灣水稻上之害蟲，惟日後野外調查亦未被發現者；(2) 屬於多食性害蟲 (polyphagous) 種類，曾被列為水稻害蟲，之後卻無報告證明者；(3) 上述 2 種害蟲種類，其幼期個體在野外被採集，並攜回實驗室或套網飼育，但無法成功存活者；(4) 曾在報告中記載為臺灣水稻害蟲種類，但證實臺灣當時並無此種害蟲存在，或寄主確定不含水稻。具上述情形者，均判定為存疑種。

結果

本研究修訂之『臺灣水稻害蟲 (蟎) 名錄』總計包含 7 目 33 科 107 種之昆蟲與 1 目 1 科 1 種之蟎類 (表 1、表 2)。另外由文獻比對、考證及實地調查之結果，共有 34 種害蟲列為存疑種，將此類害蟲排除於名錄外，其結果詳列如下：

表 1. 往昔與本研究記錄之水稻害蟲與其他有害動物種類數。
Table 1. Total number of rice pest species of Taiwan from previous studies and present study.

Taxonomic category	Total number of rice pest species				
	Miwa (1943)	Tsai (1965)	Yen (1973)	Cheng (2007)	Present study
Orthoptera	23	24	24	9	22
Blattodea	0	0	3	0	1
Hemiptera	47	55	19	27	53
Thysanoptera	1	2	1	3	3
Coleoptera	4	5	3	4	4
Lepidoptera	20	25	11	13	22
Diptera	0	0	1	2	2
Insecta	95	111	62	58	107
Arachnida	-	-	-	1	1

臺灣水稻害蟲 (蟎) 名錄修訂及存疑種之判定

日治時期 (1945 年以前)

有關臺灣水稻害蟲之報告主要有 Miwa (1943) 所著之《臺灣害蟲名彙》(表 1、表 2)，其中記載危害臺灣水稻之害蟲種類計有 5 目 (直翅目、半翅目、纓翅目、鞘翅目及鱗翅目) 30 科 95 種。經查閱臺灣物種名錄 (https://taicol.tw/zh-hant/)、Zoological Record (https://www.webofscience.com/wos/woscc/basic-search) 資料檢索、全球生物多樣性資訊機構 (GBIF) 的 GBIF Backbone Taxonomy (https://www.gbif.org/dataset/d7dddbf4-2cf0-4f39-9b2a-bb099caae36c)、EPPO Global Database (https//gd.eppo.int/) 及 CABI Digital Library (https://www.cabidigitallibrary.org/action/doSearch?ConceptID=50006) 等資料庫，其中直翅目 (Orthoptera) 蝗科 (Acrididae) 方異距蝗 (*Heteropternis respondens* (Walker, 1859)) 等 14 種列為存疑種。

臺灣光復 (1945 年以後) 至今研究資料之考證

1945 年以後有關臺灣水稻害蟲名錄之報告，包含 Tsai (1965)、Yen (1973) 及 Cheng (2007) 等。Tsai (1965) 所著《臺灣植物害蟲名彙》專書，記錄可為害水稻害蟲種類 5 目 (直翅目、半翅目、纓翅目、鞘翅目及鱗翅目) 33 科 111 種，該書之引用文獻在序文中表明以 Miwa (1943)《臺灣害蟲名彙》為主，並收集 1945 年以後學者所發表的新紀錄種，只是新紀錄種之害蟲種類並未標明引用報告出處。經比對 Miwa (1943) 與 Tsai (1965) 之記載名錄害蟲種類中，發現 Tsai (1965) 的報告中增列直翅目 (Orthoptera) 螻蛄科 (Gryllotalpidae) 的臺灣螻蛄 (*Gryllotalpa formosana* Shiraki, 1930) 等 18 種。在增列的種類中，直翅目 (Orthoptera) 蟋蟀科 (Gryllidae) 的米卡鬥蟋 (*Velarifictorus micado* (Saussure, 1877)) 等 11 種，並未有危害水稻之報告，符合『某些屬於多食性昆蟲種類，於臺灣從無研究報告證明可危害水稻，但在某些名錄上列為水稻害蟲』之存疑種方式處理，這些種類列為臺灣水稻害蟲之存疑種 (附錄)。Yen (1973) 所編著《臺灣水稻之害蟲》一書內容為諸多臺灣學者整理相關報告而成，共記錄為害水稻害蟲種類 7 目 17 科 62 種，報告中增列蜚蠊目 (Blattodea) 白蟻科 (Termitidae) 的黑翅土白蟻 (*Odontotermes formosanus* (Shiraki, 1909)) 等 19 種，但經查詢上述資料庫，其中蜚蠊目 (Blattodea) 白蟻科 (Termitidae) 的新渡戶歪白蟻 (*Pericapritermes nitobei* (Shiraki, 1909)) 等 7 種並未有危害水稻之報告，故列為

表 2.　臺灣水稻害蟲 (蟎) 名錄。

Table 2.　An annotated checklist of rice insect pests and mites from Taiwan.

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
ARACHNIDA	蛛形綱			
TROMBIDIFORMES	絨蟎目			
1. Tarsonemidae	細蟎科			
(1) S*teneotarsonemus spinki* Smiley, 1967	Panicle rice mites, Rice tarsonemid mite/稻細蟎	Cheng (2007)	L, F, G	Major
INSECTA	昆蟲綱			
ORTHOPTERA	直翅目			
1. Acrididae	蝗科			
(1) *Acrida cinerea* (Thunberg, 1815)	Oriental longheaded grasshopper/尖頭蝗、中華劍角蝗	Miwa (1943); Tsai (1965:9); Yen (1973)	L	Minor
(2) *Acrida formosana* Steinmann, 1963	Taiwan cone-headed grasshopper/臺灣劍角蝗	Yen (1973)	L	Minor
(3) *Aiolopus thalassinus tamulus* (Fabricius, 1798)	European locust/斑蝗	Miwa (1943); Tsai (1965:9); Yen (1973)	L	Minor
(4) *Gastrimargus marmoratus* (Thunberg, 1815)	Band-winged grasshopper/車蝗	Yen (1973)	L	Minor
(5) *Gelastorhinus rotundatus* Shiraki, 1910	Slant-faced grasshopper/圓翅蜢蚸蝗、臺灣擬尖頭蝗	Yen (1973)	L	Minor
(6) *Gesonula punctifrons* (Stål, 1861)	擬稻蝗	Miwa (1943); Tsai (1965:11); Yen (1973)	L	Minor
(7) *Locusta migratoria migratorioides* (Reiche & Fairmaire, 1849)	Migratory locust/菲律賓飛蝗、東亞飛蝗	Miwa (1943); Tsai (1965:11); Yen (1973)	L, G	Minor
(8) *Oedaleus infernalis* Saussure, 1884	Band-winged grasshopper/黃脛小車蝗、擬車蝗	Miwa (1943); Tsai (1965:11); Yen (1973)	L	Minor
(9) *Oxya chinensis* (Thunberg)	Rice grasshopper/稻蝗	Yen (1973); Cheng (2007)	L	Minor
(10) *Oxya intricata* (Stål, 1861)	Small rice grasshopper/小蝗、小稻蝗	Miwa (1943); Tsai (1965:11); Yen (1973); Cheng (2007)	L, G	Minor
(11) *Oxya japonica* (Thunberg, 1815)	Japanese grasshopper/日本稻蝗	Cheng (2007)	L	Minor
(12) *Patanga succincta* (Johannson, 1763)	Bombay locust/條背土蝗	Miwa (1943); Tsai (1965:12); Yen (1973); Cheng (2007)	L	Minor

表 2. 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
(13) *Phlaeoba formosana* (Shiraki, 1910)	細小翅蝗、臺灣佛蝗	Miwa (1943); Tsai (1965:12); Yen (1973)	L	Minor
(14) *Stenobothrus formosanus* Shiraki, 1910	臺灣草地蝗	Miwa (1943); Tsai (1965:13); Yen (1973)	L	Minor
(15) *Stenocatantops splendens* (Thunberg, 1815)	白條細蝗	Miwa (1943); Tsai (1965:10); Yen (1973)	L, G	Minor
2. Pyrgomorphidae	錐頭蝗科			
(16) *Atractomorpha sinensis* Bolívar, 1905	中華負蝗、短額負蝗	Miwa (1943); Tsai (1965:9–10); Yen (1973)	L	Minor
3. Gryllidae	蟋蟀科			
(17) *Gryllus bimaculatus* De Geer, 1773	Two-spotted cricket/黃斑黑蟋蟀、雙斑蟋蟀	Miwa (1943); Tsai (1965:14)	L, R	Minor
(18) *Loxoblemmus arietulus* Saussure, 1877		Miwa (1943); Tsai (1965:15)	L, R	Minor
(19) *Teleogryllus mitratus* (Burmeister, 1838)	白緣眉紋蟋蟀	Miwa (1943); Tsai (1965:15)	L, R	Minor
(20) *Velarifictorus aspersus* (Walker, 1869)	長顎鬥蟋	Miwa (1943)	L, R	Minor
4. Gryllotalpidae	螻蛄科			
(21) *Gryllotalpa formosana* Shiraki, 1930	Mole cricket/臺灣螻蛄	Tsai (1965:16–17)	R	Minor
(22) *Gryllotalpa orientalis* Brumeister, 1839	Oriental mole cricket/東方螻蛄	Cheng (2007)	R	Minor
BLATTODEA	蜚蠊目			
1. Termitidae	白蟻科			
(1) *Odontotermes formosanus* (Shiraki, 1909)	Formosan subterranean termites/臺灣土白蟻、黑翅土白蟻、臺灣白蟻、姬白蟻	Yen (1973)	S	Minor
HEMIPTERA	半翅目			
1. Pentatomidae	椿象科			
(1) *Eysarcoris ventralis* (Westwood, 1837)	White-spotted stink bug/白斑椿象、二星椿象、白星椿象	Tsai (1965:27–28); Cheng (2007)	G	Minor
(2) *Eysarcoris guttigerus* (Thunberg, 1783)	Two-spotted sesame bug/圓白斑椿象、圓白星椿象	Tsai (1965:27); Cheng (2007)	G	Minor
(3) *Lagynotomus elongatus* (Dallas, 1851)	Rice stink bug/稻椿象、白邊椿象	Miwa (1943); Tsai (1965:28); Yen (1973); Cheng (2007)	G	Minor
(4) *Megarrhamphus truncatus* (Westwood, 1837)	Shield-back bugs/大蝦殼椿象	Tsai (1965:28)	G	Minor
(5) *Menida versicolor* (Gmelin, 1790)	Rice stink bug/稻赤曼椿象	Miwa (1943); Tsai (1965:28)	G	Minor

表 **2.**　臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2.　An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
(6) *Nezara viridula* (Linnaeus, 1758)	Southern green stink bug/綠椿象、南方綠椿象	Miwa (1943); Tsai (1965:28); Yen (1973); Cheng (2007)	G	Minor
(7) *Scotinophara lurida* (Burmeister, 1834)	Black rice bug/稻黑椿象、黑椿象	Miwa (1943); Tsai (1965:29); Yen (1973); Cheng (2007)	L, S, G	Major
2. Plataspidae	龜椿象科			
(8) *Megacopta cribraria* (Fabricius 1798)	Bean plataspid/篩豆龜椿	Miwa (1943); Tsai (1965:26–27); Yen (1973)	G	Minor
3. Coreidae	緣椿象科			
(9) *Cletus bipunctatus* (Herrich-Schäffer, 1840)	Spined legume bug/菲棘緣椿象	Miwa (1943); Tsai (1965:29)	G	Minor
(10) *Cletus punctiger* (Dallas, 1852)	臺灣細針緣椿象、稻棘緣椿象	Miwa (1943); Tsai (1965:29); Yen (1973); Cheng (2007)	G	Minor
(11) *Cletus trigonus* (Thunberg, 1783)	Slender rice bug/細針緣椿象、長肩棘緣椿	Miwa (1943) Tsai (1965:29); Yen (1973); Cheng (2007)	G	Minor
4. Alydidae	蛛緣椿科			
(12) *Leptocorisa acuta* (Thunberg, 1783)	Rice seed bug, Rice ear bug/臺灣蜘蛛緣椿象、禾蛛緣椿象	Miwa (1943); Tsai (1965:29–30); Yen (1973:31); Cheng (2007)	G	Minor
(13) *Leptocorisa chinensis* Dallas, 1852	Corbett rice bug/稻蛛緣椿象、中華稻緣椿象	Yen (1973:31); Cheng (2007)	G	Minor
(14) *Leptocorisa oratoria* (Fabricius, 1794)	Rice ear bug/大稻緣椿象	Yen (1973:31)	G	Minor
(15) *Riptortus pedestris* (Fabricius, 1775)	Bean bug/點蜂緣椿、臺灣細緣椿象、黃星細緣椿象、細緣椿象	Miwa (1943); Tsai (1965:30); Yen (1973); Cheng (2007)	G	Minor
(16) *Riptortus linearis* (Fabricius, 1775)	Board-headed bug/條蜂緣椿、臺灣細緣椿象	Miwa (1943); Tsai (1965:30); Yen (1973); Cheng (2007)	G	Minor
5. Lygaeidae	長椿象科			
(17) *Eucosmetus incisus* (Walker, 1872)	大頭隆胸長椿、臺灣雙星長椿象	Miwa (1943); Tsai (1965:31); Cheng (2007)	G	Minor
(18) *Paromius gracilis* (Rambur, 1839)	短喙細長椿、稻長椿象	Miwa (1943); Tsai (1965:31)	G	Minor
6. Miridae	盲椿科			
(19) *Tinginotopsis oryzae* (Matsumura, 1910)	稻盲椿象	Miwa (1943); Tsai (1965:33); Cheng (2007)	G	Minor

表 2. 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
7. Aphrophoridae	尖胸沫蟬科			
(20) *Poophilus costalis* (Walker, 1851)	Spittle bug/嗜菊短頭脊沫蟬	Miwa (1943); Tsai (1965:33)	L	Minor
8. Cicadellidae	葉蟬科			
(21) *Cicadella viridis* (Linnaeus, 1758)	Green leafhopper/大青葉蟬	Miwa (1943); Tsai (1965:34)	L	Minor
(22) *Cofana spectra* (Distant, 1908)	White leafhopper/大白葉蟬、白翅褐脈葉蟬	Miwa (1943); Tsai (1965:34)	L	Minor
(23) *Empoascanara alami* (Ahmed, 1970)	Blue rice leafhopper/一點葉蟬、黑唇斑葉蟬	Miwa (1943); Tsai (1965:37)	L	Minor
(24) *Empoascanara circumscripta* (Matsumura, 1910)	黃綠斑葉蟬	Miwa (1943); Tsai (1965:37)	L	Minor
(25) *Empoascanara limbata* (Matsumura, 1910)	雙紋斑葉蟬	Miwa (1943); Tsai (1965:37–38)	L	Minor
(26) *Kolla atramentaria* (Motschulsky, 1859)	白邊大葉蟬	Miwa (1943); Tsai (1965:34)	L	Minor
(27) *Macrosteles alpinus* (Zetterstedt, 1828)		Miwa (1943); Tsai (1965:35)	L	Minor
(28) *Maiestas dorsalis* (Motschulsky, 1859)	Zig-zag striped leafhopper/電光葉蟬、電光浮塵子、曲紋浮塵子	Miwa (1943); Tsai (1965:35); Cheng (2007)	L, G	Major
(29) *Nephotettix cincticeps* (Uhler, 1896)	Green rice leafhopper/偽黑尾葉蟬、偽黑尾浮塵子	Yen (1973); Cheng (2007)	L, G	Minor
(30) *Nephotettix nigropictus* (Stål, 1870)	Green rice leafhopper/黑條黑尾葉蟬、黑條黑尾浮塵子	Miwa (1943); Tsai (1965:36); Yen (1973); Cheng (2007)	L, G	Minor
(31) *Nephotettix virescens* (Distant, 1908)	Green rice leafhopper/臺灣黑尾葉蟬、臺灣黑尾浮塵子	Yen (1973); Cheng (2007)	L, G	Major
(32) *Nirvana placida* (Stål, 1859)	淡色隱脈葉蟬	Miwa (1943); Tsai (1965:34–35)	L	Minor
(33) *Stroggylocephalus agrestis* (Fallén, 1806)	稻扁浮塵子	Miwa (1943); Tsai (1965:36)	L	Minor
(34) *Thaia oryzivora* Ghauri, 1962	Small yellow leafhopper, Orange rice leafhopper/白翅葉蟬	Cheng (2007)	L	Minor
(35) *Thaia subrufa* (Motschulsky, 1863)	白翅葉蟬	Miwa (1943); Tsai (1965:37)	L	Minor
9. Meenoplidae	縞飛蝨科			
(36) *Nisia carolinensis* Fennah, 1971	縞飛蝨	Miwa (1943); Tsai (1965:38)	L	Minor
10. Derbidae	長翅飛蝨科			

表 **2.** 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
(37) *Diostrombus politus* Uhler, 1896	赤長翅飛蝨	Miwa (1943); Tsai (1965:38)	L	Minor
11. Delphacidae	飛蝨科			
(38) *Laodelphax striatellus* (Fallén, 1826)	Small brown planthopper/斑飛蝨、穗飛蝨	Tsai (1965:39); Yen (1973); Cheng (2007)	L	Major
(39) *Metadelphax propinqua* (Fieber, 1866)	淡色飛蝨	Miwa (1943); Tsai (1965:38)	L	Minor
(40) *Nilaparvata lugens* (Stål, 1854)	Brown planthopper/褐飛蝨	Miwa (1943); Tsai (1965:39); Yen (1973); Cheng (2007)	L	Major
(41) *Perkinsiella sinensis* Kirkaldy, 1907	中華扁角飛蝨	Miwa (1943); Tsai (1965:40)	L	Minor
(42) *Sogatella furcifera* (Horváth, 1899)	White-backed planthopper/白背飛蝨	Miwa (1943); Tsai (1965:40); Cheng (2007)	L	Major
(43) *Tropidocephala brunnipennis* Signoret, 1860	瘤飛蝨、棕翅飛蝨	Miwa (1943); Tsai (1965:40)	L	Minor
12. Dictyopharidae	象蠟蟬科			
(44) *Raivuna patruelis* (Stål, 1859)	長頭臘蟬	Miwa (1943); Tsai (1965:38)	L	Minor
13. Cixiidae	菱飛蝨科			
(45) *Oteana oryzae* (Matsumura, 1911)	Long-nosed planthopper /稻菱飛蝨	Miwa (1943); Tsai (1965:38)	L	Minor
14. Ricaniidae	廣翅蠟蟬科			
(46) *Ricania taeniata* Stål, 1870	褐帶廣翅蠟蟬	Miwa (1943); Tsai (1965:41)	L	Minor
15. Aphididae	常蚜科			
(47) *Rhopalosiphum maidis* (Fitch, 1856)	Corn leaf aphid/玉米蚜	Miwa (1943); Tsai (1965:68); Cheng (2007)	S, L, G	Major
(48) *Rhopalosiphum padi* (Linnaeus, 1758)	Grain aphid/麥縊蚜、稻麥蚜	Cheng (2007)	S, L, G	Minor
(49) *Rhopalosiphum rufiabdominale* (Sasaki, 1899)	Rice root aphid/紅腹稻根蚜	Cheng (2007)	S, L, G	Minor
(50) *Sitobion miscanthi* (Takahashi, 1921)	Indian grain aphid/萱芒蚜	Miwa (1943); Tsai (1965:64)	S, L, G	Major
16. Pemphigidae	綿癭蚜科			
(51) *Tetraneura nigriabdominalis* (Sasaki, 1899)	Rice root aphid/稻根蚜蟲、粗長毛禾根蚜	Miwa (1943); Tsai (1965:69)	R	Minor

表 2. 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
17. Pseudococcidae	粉介殼蟲科			
(52) *Brevennia rehi* (Lindinger, 1943)	Rice mealybug/稻粉紅介殼蟲	Cheng (2007)	S, L, G	Minor
(53) *Dysmicoccus boninsis* (Kuwana, 1909)	Gray sugarcane mealybug/稻粉介殼蟲、甘蔗嫡粉介殼蟲	Miwa (1943); Tsai (1965:76)	S, L, G	Minor
THYSANOPTERA	纓翅目			
1. Phlaeothripidae	管薊馬科			
(1) *Haplothrips aculeatus* (Fabricius, 1803)	Cereal thrips, Grass thrips/稻管薊馬	Miwa (1943); Tsai (1965:23); Cheng (2007)	F, G	Minor
2. Thripidae	薊馬科			
(2) *Frankliniella intonsa* (Trybom, 1895)	Flower thrips, Taiwan flower thrips/臺灣花薊馬	Cheng (2007)	F, G	Minor
(3) *Stenchaetothrips biformis* (Bagnall, 1913)	Paddy thrips, Oriental rice thrips, Rice thrips/稻薊馬	Tsai (1965:22); Yen (1973); Cheng (2007)	L	Minor
COLEOPTERA	鞘翅目			
1. Chrysomelidae	金花蟲科			
(1) *Dicladispa armigera* (Olivier, 1808)	Rice hispa/稻鐵甲蟲	Miwa (1943); Tsai (1965:145); Yen (1973); Cheng (2007)	L	Major
(2) *Oulema oryzae* (Kuwayama, 1931)	Rice leaf beetle/稻負泥蟲	Miwa (1943); Tsai (1965:147); Yen (1973); Cheng (2007)	L	Major
2. Curculionidae	象鼻蟲科			
(3) *Echinocnemus squameus* (Billberg, 1820)	Rice plant weevil/水稻象鼻蟲	Miwa (1943); Tsai (1965:149); Yen (1973); Cheng (2007)	L, R	Major
(4) *Lissorhoptrus oryzophilus* Kuschel, 1952	Rice water weevil/水稻水象鼻蟲	Cheng (2007)	L, R	Major
LEPIDOPTERA	鱗翅目			
1. Crambidae	草螟科			
(1) *Ancylolomia chrysographellus* (Kollar & Redtenbacher, 1844)	Angled grass moth	Miwa (1943); Tsai (1965:103)	L	Minor
(2) *Chilo suppressalis* (Walker, 1863)	Striped rice stem borer, Rice stem borer/二化螟、稻條螟	Miwa (1943); Tsai (1965:103); Yen (1973); Cheng (2007)	L, S	Major

表 2. 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
(3) *Chilo auricilius* Dudgeon, 1905	Gold-fringed rice stem borer/臺灣稻螟蛾	Miwa (1943); Tsai (1965:103); Yen (1973)	L	Minor
(4) *Cnaphalocrocis medinalis* (Guenée, 1854)	Rice leaffolder, Rice leafroller/瘤野螟、水稻縱捲葉蟲	Miwa (1943); Tsai (1965:105); Yen (1973); Cheng (2007)	L	Major
(5) *Parapoynx stagnalis* (Zeller 1852)	Rice caseworm, Rice case bearer/白水螟蛾	Miwa (1943); Tsai (1965:105)	L, S	Minor
(6) *Parapoynx fluctuosalis* (Zeller, 1852)	Fluctuating China-mark, Waved China-mark/波緣帶紋水螟、稻筒水螟	Miwa (1943); Tsai (1965:105)	L	Minor
(7) *Scirpophaga incertulas* (Walker, 1863)	Paddy borer, Yellow rice borer, Yellow stem borer/三化螟、一點大螟、黃螟	Miwa (1943); Tsai (1965:103); Cheng (2007)	L	Major
2. Noctuidae	夜蛾科			
(8) *Mythimna loreyi* (Duponchel, 1827)	False army worm, Nightfeeding rice armyworm/羅氏秘夜蛾	Miwa (1943); Tsai (1965:114)	L	Minor
(9) *Mythimna separata* Walker, 1865	Paddy armyworm/分秘夜蛾、粘蟲	Miwa (1943); Tsai (1965:114)	L	Minor
(10) *Naranga aenescens* Moore, 1881	Rice green caterpillar, Rice green semilooper/稻螟蛉、紅帶黃夜蛾	Miwa (1943); Tsai (1965:115); Yen (1973); Cheng (2007)	L	Second
(11) *Naranga diffusa* (Walker, 1865)	Rice green semilooper	Yen (1973)	L	
(12) *Sesamia inferens* (Walker, 1856)	Purple stem borer, Pink borer/大螟、紫螟、盜污陰夜蛾、稻蛀莖夜蛾	Miwa (1943); Tsai (1965:115); Yen (1973); Cheng (2007)	L, S	Major
(13) *Spodoptera litura* (Fabricius, 1775)	Tobacco cutworm, Cotton leafworm/斜紋夜蛾	Cheng (2007)	L	Minor
(14) *Spodoptera mauritia* (Boisduval, 1833)	Lawn armyworm, Paddy swarming caterpillar/臺灣夜盜、劍斜紋夜蛾	Miwa (1943); Tsai (1965:115); Yen (1973); Cheng (2007)	L	Major
3. Erebidae	裳蛾科			
(15) *Cifuna locuples* Walker, 1855	Bean tussock moth/腎毒蛾	Miwa (1943); Tsai (1965:117)	L	Minor
(16) *Psalis pennatula* (Fabricius, 1793)	Yellow hairy caterpillar, hairy rice caterpillar/甘蔗毒蛾、鉤毒蛾	Miwa (1943); Tsai (1965:117)	L	Minor
4. Hesperiidae	挵蝶科			
(17) *Borbo cinnara* (Wallace, 1866)	Rice swift, Formosan swift/臺灣挵蝶、曲紋稻挵蝶	Miwa (1943); Tsai (1965:124); Yen (1973); Cheng (2007)	L	Minor
(18) *Parnara bada* (Moore, 1878)	African straight, Straight swift/廣紋稻挵蝶、東亞廣紋稻苞蟲、小稻挵蝶	Miwa (1943); Tsai (1965:124)	L	Minor

表 2. 臺灣水稻害蟲 (蟎) 名錄。(續)

Table 2. An annotated checklist of rice insect pests and mites from Taiwan. (continued)

Taxonomic category/Scientific name	Preferred common name: English/Chinese	Cited reference with information of rice insect pests and mites from Taiwan	Associated with rice root (R), stem (S), leaf (L), flower (F) or grain (G)	Category of pest
(19) *Parnara guttatus* (Bremer & Grey, 1852)	Rice skipper, Paddy skipper/稻苞蟲、稻挵蝶、直紋稻挵蝶	Miwa (1943); Tsai (1965:124); Yen (1973); Cheng (2007)	L	Minor
(20) *Pelopidas mathias* (Fabricius, 1798)	Dark small-branded swift, Small branded swift, Rice skipper/隱紋稻挵蝶、臺灣稻挵蝶	Miwa (1943); Tsai (1965:124); Cheng (2007)	L	Minor
5. Nymphalidae	蛺蝶科			
(21) *Melanitis leda* (Linnaeus, 1758)	Rice satyrid, Satyrid butterfly/水稻蛇目蝶、淡色樹蔭蝶	Miwa (1943); Tsai (1965:126); Yen (1973); Cheng (2007)	L	Minor
(22) *Mycalesis gotama nanda* Fruhstorfer, 1908	Chinese bush brown/日月蝶、姬蛇目蝶、稻眉眼蝶	Tsai (1965:127); Cheng (2007)	L	Minor
DIPTERA	雙翅目			
1. Agromyzidae	潛蠅科			
(1) *Pseudonapomyza asiatica* Spencer, 1961	Rice leaf miner/亞洲潛葉蠅、亞洲擬菁潛蠅	Cheng (2007)	L	Minor
2. Ephydridae	水蠅科			
(2) *Hydrellia philippina* Ferino, 1968	Rice leafwhorl maggot/稻心蠅、稻桿蠅	Yen (1973); Cheng (2007)	L, S	Minor

存疑種。Cheng (2007)《植物保護圖鑑系列 8- 水稻保護 (上冊)》一書除以 Tsai (1965) 報告為參考資料外，另以其他學者發表資料加以整理彙整，書籍記錄為害水稻害蟲種類 6 目 22 科 58 種與蟎類 1 目 1 科 1 種，報告中增列的直翅目 (Orthoptera) 蝗科 (Acrididae) 的日本稻蝗 (*Oxya japonica* (Thunberg, 1815)) 等 10 種害蟲與絨蟎目 (Trombidiformes) 細蟎科 (Tarsonemidae) 的稻細蟎 (*Steneotarsonemus spinki* Smiley, 1967) 1 種，經查詢上述資料庫後，直翅目 (Orthoptera) 錐頭蝗科 (Pyrgomorphidae) 的臺灣負蝗 (*Atractomorpha psittacina* (Haan, 1842)) 等 2 種並未有危害水稻之報告而被列於存疑種 (附錄)。而近年於嘉義地區有機水稻田長期監測調查結果，水稻害蟲種類間 (包含遷移性害蟲) 族群發生雖然彼此有消長，但未發現新興害蟲種類之出現。

討論

臺灣早期農田灌溉設施不發達，水稻栽培以耐旱的陸稻 (upland rice) 或秈稻 (indica variety) 為主，加上水稻種植期混雜 (Huang 1999)，害蟲發生種類繁多且危害嚴重，特別是單食性種類 (如三化螟蟲 *Scirpophaga incertulas* Walker, 1863) (Miwa 1943; Tsai 1965)；日治後期至臺灣光復期間，水利灌溉系統的大量修築且覆蓋面積廣，水稻種植品種也逐漸轉變為需大量水源灌溉的稉稻 (japonica variety)，蟲害的發生以半水生昆蟲 (semiaquatic insect) 為主，加上此時期為水稻增產期，配合化學合成肥料的大量施用，更創造出適合水稻害蟲孳生繁衍的環境，雖然有化學藥劑的防治，其他次要害蟲的崛起仍絡繹不絕，如飛蝨類與黑尾葉蟬等 (Yen 1973; Cheng & Chu 1999; Cheng 2007)；1984 年後，因國內水稻生產過剩而進行稻田轉作政策，水稻蟲害防治轉以生態為基礎之綜合管理，後期水稻害蟲除人為引進之外來入侵種 (如水稻水象鼻蟲) 與遷移性害蟲種類 (如褐飛蝨、白背飛蝨及水稻縱捲葉蟲) 族群消長略有變化外，害蟲相大致相同 (Cheng 2007; Huang *et al.* 2010)，近年田間調查蟲害之結果也顯示種類發生沒有改變。害蟲名錄之重新審定除提供害蟲發生紀錄外，並配合耕作環境、品種及政策的改變與蟲害發生更迭等資料，提供生態分析與管理之參考，也提供臺灣未來糧食安全管理策略擬定之參考資訊。

惟近年來全球暖化，臺灣之氣候環境由原本之亞熱帶，將逐漸轉變成熱帶氣候，也因此逐漸變成適合南洋地區熱帶水稻害蟲之入侵與立足 (Lai *et al.* 2023)，例如亞洲水稻癭蚋 (gall midge, *Orseolia oryzae* (Wood-Mason))、水稻螟蛾類 (水稻白螟蟲 (rice white borer, *Scirpophaga innotata* (Walker)) 及馬來亞黑椿象等。在東南亞地區，部分害蟲已有報告族群大發生且逐漸向北擴散之現象 (Sharma 2016; Lai *et al.* 2023)，臺灣也應特別注意此等害蟲之入侵並加強檢疫，避免害蟲種類發生急劇變化，進而威脅臺灣稻作安全生產。

誌謝

本研究承農業部科技計畫 (109 農科-21.5.1 -農-C3) 經費支持，感謝農業部農業試驗所嘉義分所植物保護系作物蟲害管理研究室同仁楊雪鳳小姐、吳美璇小姐、蕭繡琴小姐及賴錦雲小姐等辛勞的協助試驗調查等工作，在此一併致謝。

引用文獻

Cheng, C. H. (ed.). 2007. Compendium of Rice Diseases and Pests (I). Bureau of Animal and Plant Health Inspection and Quarantine, Council of Agriculture. Taipei, Taiwan. 280 pp. (in Chinese)

Cheng, C. H. and Y. I. Chu. 1999. The rice insect pests and its control. p.423–466. *in*: The Development History of Rice in Taiwan. (Chang, T. C. and T. T. Huang, eds.) Department of Agriculture and Forestry, Taiwan Provincial Government. Nantou, Taiwan. 793 pp. (in Chinese)

Cheng, C. H. and S. H. Huang. 2009. Reconsideration of the rice insect pests control in Taiwan. p.65–82. *in*: Proceedings of Symposium on Achievements and Perspectives of Rice Protection in Taiwan. July 9, 2009. Chiayi, Taiwan. Taiwan Agric. Res. Inst. Taichung, Taiwan. (in Chinese with English abstract)

Huang, S. H., C. H. Cheng, and W. J. Wu. 2010. Possible impacts of climate change on rice insect pests and management tactics in Taiwan. Crop. Environ.

Bioinform. 7:269–279. (in Chinese with English abstract) doi:10.30061/CEB.201012.0006

Huang, T. T. 1999. Overview of rice production and policy evolution in Taiwan. p.19–42. *in*: The Development History of Rice in Taiwan. (Chang, T. C. and T. T. Huang, eds.) Department of Agriculture and Forestry, Taiwan Provincial Government. Nantou, Taiwan. 793 pp. (in Chinese)

Lai, P. Y., Y. B. Huang, Y. J. Dong, Li-Hsin Wu, and S. H. Huang. 2023. Climate change mitigation strategies of rice insect pests in Taiwan. J. Taiwan Agric. Res. 72:277–287. (in Chinese with English abstract) doi:10.6156/JTAR.202312_72(4).0001

Miwa, Y. 1943. A Handlist of Pest Insects in Formosa. Publ. No. 16. Taiwan Farmer's Association. Taipei, Taiwan. 242 pp. (in Japanese)

Pena, J. E., A. I. Mohyuddin, and M. Wysoki. 1997. The current mango pests management in the tropics and subtropics. Acta Hortic. 455:812–820. doi:10.17660/ActaHortic.1997.455.103

Sharma, H. C. 2016. Climate change *vis-a-vis* pest management. p.17–25. *in*: Conference on National Priorities in Plant Health Management. Tirupati, India. 230 pp.

Shih, H. T., H. H. Hao, Y. C. Chiu, F. C. Lin, and M. M. Yang. 2013. A revised and annotated checklist of insect and mites of mangos from Taiwan. Formosan Entomol. 33:27–51. (in Chinese with English abstract) doi:10.6661/TESFE.2013003

Tsai, Y. P. 1965. List of Phytophagous Insect Pests in Taiwan. Bureau of Commodity Inspection and Quarantine. Taipei, Taiwan. 278 pp. (in Chinese)

Yen, F. Y. 1973. The rice insect pests in Taiwan. Department of Plant Pathology and Entomology, National Taiwan University. Taipei, Taiwan. 172 pp. (in Chinese)

附錄 . 臺灣水稻害蟲之存疑種清單。

Appendix. A list of questionable species of rice pests in Taiwan.

Orthoptera

Acrididae

1. *Heteropternis respondens* (Walker, 1859)
2. *Oxya hyla* Serville, 1831
3. *Oxya velox* (Fabricius, 1787)
4. *Oxya vicina* Brunner von Wattenwyl, 1893
5. *Phlaeoba sinensis* Bolívar, 1914
6. *Traulia ornata* Shiraki, 1910
7. *Trilophidia annulata* (Thunberg, 1815)
8. *Xenocatantops humilis* (Serville, 1838)

Pyrgomorphidae

9. *Atractomorpha lata* (Mochulsky, 1866)
10. *Atractomorpha psittacina* (Haan, 1842)

Gryllidae

11. *Velarifictorus micado* (Saussure, 1877)

Trigonidiidae

12. *Pteronemobius caudatus* (Shiraki, 1911)
13. *Trigonidium cicindeloides* Rambur, 1838

Blattodea

Termitidae

14. *Pericapritermes nitobei* (Shiraki, 1909)
15. *Sinocapritermes mushae* (Oshima & Maki, 1919)

Hemiptera

Aphididae

16. *Sitobion avenae* Fabricius, 1794

Pentatomidae

17. *Andrallus spinidens* (Fabricius, 1787)
18. *Megarrhamphus hastatus* (Fabricius, 1803)

Plataspidae

19. *Megacopta punctatissima* (Montandon, 1896)

Coreidae

20. *Paradasynus spinosus* Hsiao, 1963

Miridae

21. *Lygus sacchari* Matsumura 1910

Dictyopharidae

22. *Raivuna sinica* (Walker, 1851)

Achilidae

23. *Usana yanonis* Matsumura, 1914

Cicadellidae

24. *Ishidaella albomarginata* (Signoret, 1853)

附錄． 臺灣水稻害蟲之存疑種清單。(續)

Appendix. A list of questionable species of rice pests in Taiwan. (continued)

25. *Macrosteles sexnotatus* (Fallén, 1806)
26. *Scaphoideus albovittatus* Matsumura, 1913
27. *Scaphoideus festivus* Matsumura, 1902

Coleoptera

Chrysomelidae

28. *Donacia lenzi* Schonfeldt, 1888

Anthicidae

29. *Anthelephila bramina* (LaFerté-Séneetère, 1849)

Lepidoptera

Hesperiidae

30. *Pelopidas sinensis* (Mabille, 1877)
31. *Suastus gremius* Fabricius, 1798
32. *Telicota bambusae horisha* Evans, 1934

Nymphalidae

33. *Melanitis phedima polishana* Fruhstorfer, 1908
34. *Mycalesis francisca* Cramer, 1782

A Revised Checklist of Insects and Mites of Rice from Taiwan

Shou-Horng Huang[1], Po-Yu Lai[2,*], and Tai-Chuan Wang[3,*]

Abstract

Huang, S. H., P. Y. Lai, and T. C. Wang. 2025. A revised checklist of insects and mites of rice from Taiwan. J. Taiwan Agric. Res. 74(2):189–204.

Rice is the staple crop in Taiwan, and the safe production of rice is crucial for the well-being of its people and national security. Establishing the rice pest checklist is important to provide information for pest ecology and management tactics. The recorded number of rice insect pests has varied from 59 to 111 species. After the revision, there were 107 species of insects and 1 species of mite currently, and 34 species, such as short-horned grasshopper (*Heteropternis respondens* (Walker, 1859)), were considered as dubious and excluded in the present checklist.

Key words: Taiwan, Rice, Checklist of insects and mites.

Received: December 3, 2024; Accepted: February 11, 2025.
* Corresponding author, e-mail: tukust94413@tari.gov.tw; insect6925@mail.kdais.gov.tw
1 Associate Research Fellow and Division Director, Department of Plant Protection, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.
2 Assistant Research Fellow, Department of Plant Protection, Chiayi Agricultural Experiment Branch, Taiwan Agricultural Research Institute, Chiayi, Taiwan, ROC.
3 Assistant Research Fellow, Crop Environment Section, Kaohsiung District Agricultural Research and Extension Station, Pingtung County, Taiwan, ROC.

Editorial Board

Editor-in-Chief

Shih, Hsien-Tzung
Division of Applied Zoology, Taiwan Agricultural Research Institute

Deputy Editor-in-Chief

Syu, Chien-Hui
Division of Agricultural Chemistry, Taiwan Agricultural Research Institute
Wu, Dong-Hong
Division of Crop Science, Taiwan Agricultural Research Institute

Editors

Ann, Pao-Jen
Division of Plant Pathology, Taiwan Agricultural Research Institute
Chang, Ruey-Jang
Agricultural Chemicals Research Institute
Chang, Yung-Ho
Department of Food and Nutrition, Providence University
Chen, Chien-Chung
Division of Applied Zoology, Taiwan Agricultural Research Institute
Chen, Chiling
Division of Agricultural Chemistry, Taiwan Agricultural Research Institute
Chen, Iou-Zen
Department of Horticulture and Landscape Architecture, National Taiwan University
Chen, Suming
Department of Bio-Industrial Mechatronics Engineering, National Taiwan University
Chung, Wen-Hsin
Department of Plant Pathology, National Chung Hsing University
Do, Yi-Yin
Department of Horticulture and Landscape Architecture, National Taiwan University
Hou, Feng-Nan
Department of Entomology, National Chung Hsing University
Huang, Biing-Wen
Department of Applied Economics, National Chung Hsing University
Huang, Chao-Chia
Division of Crop Science, Taiwan Agricultural Research Institute
Huang, Jenn-Wen
Department of Plant Pathology, National Chung Hsing University
Huang, Yuh-Ming
Department of Soil and Environmental Sciences, National Chung Hsing University
Juang, Kai-Wei
Department of Agronomy, National Chung Hsing University
Ku, Hsin-Mei
Department of Agronomy, National Chung Hsing University
Kuo, Bau-Jeng
Department of Agronomy, National Chung Hsing University
Lin, Huey-Ling
Department of Horticulture, National Chung Hsing University
Lin, Yann-Rong
Department of Agronomy, National Taiwan University
Liu, Li-Yu
Department of Agronomy, National Taiwan University
Lu, Hsiu-Ying
Miaoli District Agricultural Research and Extension Station
Lu, Kuang-Hui
Department of Entomology, National Chung Hsing University
Tsay, Jyh-Rong
Taiwan Agricultural Research Institute
Tzou, Yu-Min
Department of Soil and Environmental Sciences, National Chung Hsing University
Wang, Chan-Sen
Department of Agronomy, National Chung Hsing University
Yang, Chwen-Ming
Division of Crop Science, Taiwan Agricultural Research Institute
Yang, Jeng-Tze
Department of Entomology, National Chung Hsing University
Yen, Gow-Chin
Department of Food Science and Biotechnology, National Chung Hsing University

English Editorial Board

Chang, Chung-Jan
Department of Plant Pathology, University of Georgia, USA
Chung, Kuang-Ren
Department of Plant Pathology, National Chung Hsing University
Wang, Yin-Tung
Department of Horticultural Sciences, Texas A&M University, USA
Yang, Chin-Cheng Scotty
Department of Entomology, Virginia Polytechnic Institute and State University, USA

Editorial Assistants

Wang, Li-Jung
Editorial Office of Journal of Taiwan Agricultural Research

JOURNAL OF TAIWAN AGRICULTURAL RESEARCH

Vol. 74 No. 2 June 30, 2025

Published by Taiwan Agricultural Research Institute, Ministry of Agriculture

Publisher Hsueh-Shih Lin
Editor-in-Chief Hsien-Tzung Shih
Address No.189, Zhongzheng Rd., Wufeng Dist., Taichung City 413008, Taiwan, ROC
Website https://www.tari.gov.tw/jtar; E-mail: jtar@tari.gov.tw; Tel: +886-4-2331-7236
Submission https://www.ipress.tw/J0042
Complete instructions to authors are available on Journal of Taiwan Agricultural Research website: https://www.tari.gov.tw/jtar/

Press Ainosco Press
Address 18F, No.80, Sec.1, Chenggong Rd., Yonghe Dist., New Taipei City 234634, Taiwan, ROC
Tel +886-2-2926-6006
E-mail press@airiti.com

Price NT$ 175 (per copy)
Distributor 1. GB Books / 1F., No.209, Songjiang Rd., Taipei City 104472, Taiwan, ROC
GB Website: http://www.govbooks.com.tw; Tel: +886-2-2518-0207
2. Wunan Books / No.6, Zhongshan Rd., Taichung City 400002, Taiwan, ROC; Tel: +886-4-2226-0330